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DISSERTATION

Effects of Seasonality on the Productivity of Pastoral Goat Herds in Northern Kenya

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Summary

Under semi-arid rangeland conditions in northern Kenya, the main factor influencing the productivity of small ruminant flocks is climatic seasonality. In pastoral production systems, alternatives to herd mobility as an efficient adaptive management strategy to overcome nutritional deficits are few. One possible intervention is to manipulate the total seasonal nutrient requirements of the herd through controlled seasonal breeding, which commonly is not practised by pastoralists.

The restriction of breeding as a management strategy to match periods of critical nutrient demands with seasonal feed supply in pastoral goat flocks has so far received little attention in research. In order to gain a clearer understanding of the merits and demerits of controlled seasonal breeding, a systematic breeding programme in a herd of Small East African goats was initiated for a period of four years (1984-1988) in Isiolo District, northern Kenya. The study was undertaken to (1) assess the effect of seasonal forage supply on various parameters determining pastoral goat flock performance, and (2), using these baseline data, to test the hypothesis that a seasonally restricted breeding regime can increase flock productivity.

A total of 145 does of the Small East African type were maintained under simulated pastoral management conditions and used for a total of 381 exposures which were distributed among 18 consecutive breeding groups consisting of approximately 18 does each. The experimental design resulted in six different, consecutive mating periods or seasons per year, which were replicated three times during the course of the experiment. A total of 8547 recordings were obtained on survival, liveweight, and milk production of does; 9837 observations were available on survival and liveweight development of youngstock. Detailed statistical analyses were performed on all traits relevant to assessing overall biological herd productivity, including: survival of kids and does; reproductive performance of does; growth performance of kids and body weight development of does; and milk production. A steady-state herd model was developed and used to assess overall flock productivity for each of the six consecutive two-month breeding seasons. The procedure is based on a stage-specific description of population dynamics and uses non-linear programming to derive the steady-state herd structure and culling policy that maximizes overall energetic efficiency of the herding enterprise.

Mating season had no statistically significant effect on reproduction traits, most likely due to the large variability in within-season environmental conditions among the three production cycles. Differences in kid survival among mating seasons were marked. The results demonstrated that restricted breeding can be an effective means to control kid mortality. Similar conclusions apply with respect to milk yield, which was an important risk factor affecting kid survival until weaning. Although growth performance of kids until weaning differed substantially among mating seasons, these had largely disappeared by one year of age. Therefore, seasonal breeding does not seem to confer any major advantage in terms of growth performance of youngstock per se.

Steady-state herd productivity assessments revealed that under the current production conditions reproductive performance traits are far less important as contributors to biological productivity than is often assumed. Sensitivity analyses showed that juvenile survival rate is the most important factor determining overall energetic efficiency. Restricted breeding can be used as a management control to manipulate overall biological herd productivity primarily because of its positive effect on youngstock mortality rates. In contrast, yield levels, i.e., growth and milk performance, are less important as determinants of biological herd productivity, once their effect on youngstock mortality has been accounted for. Joining does at the peak of the long dry season (July and August) proved to be the optimal management strategy in terms of energetic efficiency at the herd level. Whether restricted breeding is biologically superior to an aseasonal breeding management, as is often practised by pastoral producers, remains ambiguous. The results for a simulated aseasonal breeding regime indicated that the potential improvements in biological productivity are probably much smaller than is usually presumed.

With respect to steady-state herd productivity assessment, results of the present work emphasized the importance of utilizing an optimality approach for obtaining a common basis on which management alternatives can be compared in terms of their effect on energetic efficiency at the herd level. The assessment procedure is essentially a device with which standardized comparisons of biological or economic productivity in livestock herds can be carried out, but it can also be a valuable aid in understanding or optimising the production system looked at.

Keywords: seasonality; herd productivity; goats; pastoral systems.

Zusammenfassung

Der wichtigste Bestimmungsfaktor für die Produktivität in der Herdenhaltung kleiner Wiederkäuer unter semi-ariden Weidebedingungen ist die klimatisch bedingte Saisonalität im Futteraufwuchs. In pastoralen Produktionssystemen gibt es nur wenige Alternativen zur Mobilität als effiziente und angepaßte Strategie zur Überwindung von Nährstoffdefiziten. Eine denkbare Intervention bestünde darin,, den saisonalen Nährstoffbedarf der Herde über ein kontrolliertes Anpaarungsmanagement zu steuern. Eine derartige Strategie wird jedoch von pastoralen Produzenten üblicherweise nicht durchgeführt.

Restriktives Anpaarungsmanagement als ein Mittel zur Synchronisation der Nährstoffansprüche pastoraler Ziegenherden mit dem saisonalen Futterangebot hat bisher in der Forschung nur wenig Beachtung gefunden. Um die Vor- und Nachteile einer kontrollierten saisonalen Anpaarung zu untersuchen, wurde über einen Zeitraum von vier Jahren (1984-1988) im Isiolo Distrikt im Norden Kenias ein systematisches Anpaarungsprogramm in einer Herde kleiner Ostafrikanischer Ziegen durchgeführt. Ziel der Studie war es, (1) den Effekt einer saisonalen Anpaarung auf wichtige Leistungsmerkmale von Ziegenherden zu untersuchen, und (2) diese Daten für den Test der Hypothese zu verwenden, daß ein restriktives saisonales Anpaarungsmanagement die Produktivität pastoraler Ziegenherden zu steigern vermag.

Es wurden 145 Muttertiere auf 18 aufeinander folgende Anpaarungsgruppen mit jeweils ca. 18 Tieren verteilt und für insgesamt 381 Anpaarungen verwendet. Jeder dieser 18 Gruppen wurde über einen Zeitraum von 2 Monaten der gleiche Zuchtbock zugeführt. Aus dem experimentellen Design ergaben sich 6 Anpaarungsperioden pro Jahr, die jeweils dreimal im Verlauf des Experiments wiederholt wurden. Es wurden 8547 Messungen bezüglich der Mortalität, der Gewichtsentwicklung und Milchleistung der Muttertiere erhoben; 9337 Messungen wurden zur Mortalität und Wachstumsleistung der Jungtiere erhoben. Statistische Analysen wurden für alle relevanten Leistungsmerkmale durchgeführt. Dazu zählen die Überlebensleistung von Jung- und Muttertieren, die Reproduktionsleistung der Muttertiere, die Wachstumsleistung der Jungtiere, sowie die Gewichtsentwicklung und Milchleistung der Mütter. Für die Ermittlung der Herdenproduktivität in den sechs Anpaarungsperioden wurde ein neues steady-state Herdenmodell entwickelt. Dieses Verfahren basiert auf einer zustandsstrukturierten Beschreibung der Populationsdynamik und verwendet einen nicht linearen Optimierungsansatz zur simultanen Bestimmung der steady-state-Herdenstruktur und der Merzpolitik, die die energetische Effizienz auf Herdenebene maximiert.

Die Anpaarungsperiode hatte keinen signifikanten Effekt auf Reproduktionsmerkmale, was höchstwahrscheinlich auf die hohe Variabilität in den Produktionsbedingungen zwischen den drei Wiederholungen einer Periode zurückzuführen ist. Die Unterschiede in der Überlebensleistung der Jungtiere zwischen den Anpaarungsperioden waren stark ausgeprägt. Die Ergebnisse belegen, daß restriktive Anpaarung ein effektives Mittel zur Reduzierung der Jungtiersterblichkeit sein kann. Ähnliche Schlußfolgerungen gelten in Bezug auf die Milchleistung. Die anfänglichen Unterschiede in der Wachstumsleistung zwischen den Anpaarungsperioden verschwanden weitestgehend bis die Tiere das Jährlingsstadium erreicht hatten. Daher kann man davon ausgehen, daß eine saisonale Anpaarung per se keinen nennenswerten Vorteil bezüglich der Wachstumsleistung von Jungtieren verschafft.

Die ermittelten steady-state-Produktivitäten verdeutlichen, daß unter den gegebenen Bedingungen Reproduktionsleistungsmerkmale weitaus weniger bedeutsam für die biologische Herdenproduktivität sind, als dies häufig angenommen wird. Mit Hilfe von Sensitivitätsanalysen wurde gezeigt, daß die Jungtiersterblichkeit mit Abstand der wichtigste Bestimmungsfaktor für die energetische Effizienz auf Herdenebene ist. Restriktive Anpaarung kann aufgrund des positiven Einflusses auf die Überlebensleistung der Lämmer als Strategie zur Steigerung der biologischen Produktivität genutzt werden. Milch- und Wachstumsleistung sind von untergeordneter Bedeutung, nachdem ihre positiven Effekte auf die Überlebensleistung der Jungtiere berücksichtigt wurden. Eine Anpaarung auf dem Höhepunkt der langen Trockenzeit (Juli bis August) stellte die optimale Managementstrategie dar. Ob eine restriktive Anpaarung einer kontinuierlichen Anpaarung überlegen ist, konnte jedoch nicht zweifelsfrei festgestellt werden. Die Ergebnisse eines simulierten asaisonalen Managements deuten darauf hin, daß der durch saisonale Anpaarung erzielbare Effizienzzuwachs deutlich geringer ausfallen dürfte, als bisher angenommen wurde.

Bezüglich der Methode zur Ermittlung der steady-state Herdenproduktivität ist festzuhalten, daß der Verwendung eines Optimalitätsansatzes für die Schaffung einer gemeinsamen Vergleichsbasis eine herausragende Bedeutung zukommt. Der entwickelte Bewertungsansatz erlaubt die Durchführung standardisierter Effizienzvergleiche auf Herdenebene und Kann zugleich ein wertvolles Hilfsmittel für ein besseres Verständnis von Produktionssystemen, bzw. für deren Optimierung sein.

Schlagwörter: Saisonalität; Herdenproduktivität; Ziegen; pastorale Systeme.

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Chapter 1

General introduction

1.1 Background

Pasture based livestock production with domestic ruminants, dromedaries and donkeys is the dominant economic activity in the dry lowlands of Kenya. These areas are characterized by low and erratic rainfall, a high probability of droughts, as well as by a general scarcity of permanent surface water and are therefore generally unsuited to cultivation. Migratory pastoralism has evolved under these marginal production conditions and remains the most important land use system in these regions. Pastoral production systems share a number of unique characteristics that are aimed at minimizing production shortfalls caused by large variations in forage productivity. One of the most prominent risk minimising system attributes relates to the mobility of pastoral livestock herds and households, allowing full exploitation of forage resources that are unequally distributed in space and time (Coughenour et al., 1985; Ellis et al., 1988). Orientation towards subsistence production, reliance upon a combination of different animal species, considerable sharing of resources and products within small groups, and an emphasis on milk rather than meat production are additional features contributing to risk avoidance in pastoral economies (Swift, 1982; Western, 1982).

Change in migratory pastoralism: sedentarisation and commercialisation

These features have helped pastoral production systems to remain remarkably stable for a long time. However, fundamental demographic, economic, and political changes have disrupted the delicate balances between human populations, livestock numbers, and rangeland resources in these socionatural systems. These changes originated partly in programmes of the colonial administration aimed at raising productivity in the pastoral sector, which, subsequently, were taken over almost without interruption by the Kenyan government after independence (Oxby, 1975; Bennett, 1988). Attempts at restructuring pastoral production systems to increase their economic self-sufficiency and contribution to the national economy have almost always failed. Instead, such attempts have affected traditional land-use practices, have led to permanent differential access to basic productive resources, and to a substantial increase in income disparities among pastoral households (Hogg, 1986; Mayer et al., 1986). However, a more serious influence on pastoral production systems relates to the constantly increasing human population in the semi-arid rangeland areas of Kenya, and to the accompanying conflict over land resources. The rapid population growth in neighbouring agricultural communities has led to an expansion of cultivation onto semi-arid rangelands. In particular the small pockets of high potential pastoral land which formerly served as grazing reserves, are increasingly being occupied by agriculturalists. These losses have been aggravated by the establishment of commercial ranches and national parks on pastoral land (Schwartz & Schwartz, 1985). The increased competition for resources among different land use systems was also paralleled by a steady growth of the pastoral population, although at a slower rate than in other groups in Kenya, which further decreased the per capita availability of land for grazing (Swift, 1982).

The combined forces of demographic pressure, steady loss of rangeland to other sectors, and development interventions in pastoral economies have contributed to a rapid decrease in the mobility of pastoral herds and settlements throughout Kenyan rangelands (Grandin, 1988, 1991; Fratkin, 1992; Schwartz et al., 1995; Roth, 1996). Sedentary pastoralism in the vicinity of small towns, trade centres, famine relief stations, and mechanized water sources has become a widespread practice, especially among impoverished pastoral households (O'Leary, 1990). The transition to sedentarism, for long a primary objective of development policies aimed at pastoralists in Kenya, is now inevitable given the major alterations in system functions; this process is likely to cause substantial ecological and economical problems. Schwartz et al. (1995), for instance, note that concentration areas are marked by severe and spreading degradation of vegetation and soils. This, in turn, lowers herd productivity, increases herd sizes required to meet household needs, and thus further accelerates environmental degradation and the likelihood of destitution.

The sedentarisation of pastoral households is intrinsically related to the incorporation of pastoral economies into regional and national markets. Whether the observed emergence of market oriented production over traditional subsistence production is an additional cause or merely a consequence of sedentarisation remains ambiguous; both processes are generally so intertwined that it is difficult to distinguish cause and effect

(Sikina et al., 1993). Nevertheless, both processes entail a gradual change in pastoral herd management and species composition, and, ultimately, a redefinition of production goals. Several studies conducted in northern Kenya have documented changes in species composition in pastoral livestock herds arising from population increase, reduced mobility, and commercialisation of production. Roth (1990) and Roth and Fratkin (1991) observed a recent emphasis on cattle as opposed to camels in Rendille livestock herds, which is a reflection of an increasing interaction with a cash economy. The transition from camels to cattle as the predominant species is a strategy adopted by livestock wealthy Rendille households who attempt to make the shift to commercial production and to minimise losses in a changing socioeconomic environment. Although less ecologically adapted, cattle have a retail market in northern Kenya which camels lack. Due to their higher market value, cattle tend to replace camels in their function as a store of wealth and as a means for exchange purposes (Roth, 1990).

Poor Rendille households, in contrast, concentrate on smallstock. The rapid rate of reproduction of smallstock makes them a major means of post-drought recovery. Moreover, accumulation of smallstock is a sensible strategy for poor households since they are easily converted to cash for household needs, and can be utilized as a means of acquiring large stock (Roth & Fratkin, 1991). Mace and Houston (1989) arrive at similar conclusions concerning the importance of smallstock to maximising household survival chances at low herd sizes. According to Schwartz (1987), the goat has also become the main meat supplier for most pastoral consumers in northern Kenya, a fact which strongly indicates a drastic change in socioeconomic patterns in pastoral societies that have to deal pragmatically with recurring emergencies. Likewise, data presented by McCabe (1987) for the Ngisonyoka Turkana suggest a shift from a pastoral subsistence based on cattle to one based on smallstock in a situation where livestock holdings per capita are decreasing. In contrast to sheep and goats, cattle have the disadvantage of being large indivisible units, such that substantial amount of the herder's wealth is stored in only a few animals. Poor households are therefore less vulnerable to livestock losses when concentrating on smallstock, since here, the capital accumulated in each animal is minimal.

Similar patterns of change have also been observed on Maasai group ranches in southeastern Kajiado District (King et al., 1984). High population growth was accompanied by an increase in labour availability and food requirements and hence a need for a more intensive exploitation of fodder resources through species diversification. Maasai began to rear smallstock in response to adverse climatic conditions and an increase in population pressure. Sheep and goats played a critical role in maintaining domestic food supplies during the disastrous droughts in the early sixties and in the mid-seventies. Since then, a substantial increase in the smallstock population and in the importance of meat and milk from small ruminants in the Maasai diet has been observed (Njoka, 1979). However, the overall number of livestock units per capita decreased, and this induced higher levels of exchange of pastoral for agricultural foodstuffs, inputs for livestock production, and other essential goods (Grandin & Bekure, 1982; Grandin, 1988).

Patterns of smallstock and cattle utilization vary according to the scale of the operation unit. Poor Maasai producers have much greater rates of utilization of their smallstock in terms of milk, meat and especially live animal sales than rich producers. Due to their low livestock to human ratio and pressing consumption needs, poor households have to engage in market exchange in order to convert their livestock products to foodstuffs with higher energetic value (Ensminger, 1987; Grandin, 1988; Sikina et al., 1993). With respect to cattle, poor herd owners tend to rely on an intensive extraction of milk from their herds, whereas richer herders deliberately forego some of the potential milk output in favour of calves and derive higher levels of income from live animal trade. In general, poor producers attempt to offset diseconomies of scale by intensive methods of extracting value from animals (Behnke, 1984).

The case of the Maasai group ranches suggests that the growth in smallstock holdings may also be linked to a change in rangeland vegetation induced by an increase in land use pressure (Njoka, 1979). Goats in particular have a wider dietary range and lower water requirements than cattle, and are better adapted to cope with drought and poor grazing conditions such as often occurs in the vicinity of permanent settlements. King et al. (1984) report that reduced herd mobility combined with increasing livestock populations has led to significant changes in plant composition of the rangeland vegetation in Maasai group ranches, and that this change has favoured the shift towards smallstock. Likewise, Bekure and de Leeuw (1991) state that the growing grazing pressure on rangeland in southeastern Kajiado is likely to lead to the replacement of perennial grasses by bushes, dwarf shrubs, forbs and ephemeral annual grasses and encourage Maasai producers to keep more smallstock to effectively exploit forage resources. Thus, the increase of smallstock holdings especially among stock-poor households could also be interpreted as an adaptation to a degrading habitat. In general, it can be expected that those households that diversify their herds by keeping a significant proportion of sheep and goats may likely adapt more readily and securely to a sedentary lifestyle (DeVries & Pelant, 1987).

Consequences for the future of pastoral economies

From the foregoing, a number of consequences for the future of pastoral economies in Kenya can be anticipated. First, the rapid integration of pastoral economies in regional and national markets will continue to impact on management strategies and production goals of pastoral producers. The process of commercialization is, however, not neutral to scale, and will therefore affect large and small subsistence operations differently. Large herd owners can more readily accommodate the shift from in-kind milk and meat production to market oriented meat production, since the reduction in overall biological productivity implied by this shift is potentially more than offset by the higher economic profitability achieved through live animal sales (Behnke, 1984). Small operation units, in contrast, can not afford to abandon traditional subsistence forms of animal use. The potential offtake rate of live animals for sale from their herds is too low to meet the household expenses required to substitute the majority of subsistence products for non-pastoral foodstuffs. Small herd owners will therefore have to retain a predominant subsistence oriented mode of production in order to increase herd sizes for an eventual shift towards commercial production. On the other hand, the process of commercialisation has been observed to entail a reduction in the number of surplus livestock from wealthier households available for redistribution through animal loans, gifts and other transfers, thus depriving small herd owners of an important source of livestock to build up their herds (Behnke, 1983; Grandin, 1991; Moris, 1991; Sikina & Kerven, 1991). In addition, those producers who successfully make the shift to commercial production will attempt to reinforce their economic superiority by acquiring private use rights to land, a phenomenon which is already common among Maasai pastoralists in Kajiado District (Grandin, 1989; de Leeuw et al., 1984). Together, these developments will further undermine the viability of small production units and increase income disparities in pastoral societies (Bennett, 1988).

A second concern relates to the tendency of livestock herds to grow in commercialising pastoral economies, a trend which will aggravate the pressure on natural resources already exerted by the growing and sedentarising pastoral population. This is because the decline in biological productivity per animal unit in commercialising operations may force herd owners to increase their herd sizes in order to maintain overall household income levels (Behnke, 1984). On the other hand, herd owners can also benefit from economies of scale by increasing their herds, since larger herds tend to have lower per unit operating costs. Whereas under the traditional, labour intensive subsistence mode of production, herd growth is restricted by labour availability, this limitation is relaxed in a commercialising operation, so encouraging producers to increase their operations.

Lastly, the economic polarisation of pastoral societies will promote the exclusion of poor, subsistence oriented households from the pastoral sector (Swift, 1982). Households falling below the minimum livestock per capita ratio required to insure self-sufficiency have a limited set of alternative strategies to choose from in order to complement household incomes. They may either realise additional income from herding for other, wealthier households, seek for wage labour in nonpastoral activities, or abandon the pastoral economy altogether and migrate to small towns or large cities in search for employment (Fratkin & Roth, 1990). Yet, the capacity of pastoralism to absorb surplus labour from households which lack sufficient stock to support themselves independently is very limited. Additionally, in Kenya, employment opportunities outside the pastoral sector are few and pastoralists are at a comparative disadvantage in competing against the often better-educated agriculturalists (Grandin, 1989). Under these conditions, the likelihood of an increase in the number of displaced and destitute pastoralists is high.

In light of the complexity of the problems with which pastoral economies are confronted today, it would seem difficult to isolate a single development strategy that is capable of simultaneously alleviating the above mentioned social, economic and environmental concerns. The present demographic and macroeconomic conditions in Kenya prevent the relocation of large parts of the pastoral population to other sectors of the national economy. However, the exclusion of marginal operation units from the pastoral economy is unavoidable when the process of commercialisation is left unattended. Under these circumstances it is important to identify interventions that will allow stock-poor pastoralists to continue to support themselves largely through livestock-related activities without further increasing the pressure on natural resources in the rangeland areas (Grandin, 1989). Although a focus on technical alterations alone is clearly not sufficient to achieve this goal, improvements in the productivity of livestock herds are a necessary feature of any effort to (1) increase total output of operation units; (2) enhance food security of pastoral households, and (3) reduce the risk of environmental degradation.

1.2 Problem statement

Problem identification

Traditional pastoral production strategies are geared towards a balanced supply of food for human needs throughout the year without major shortages. This is best achieved through a combined milk and meat production, where milk is the mainstay of the diet, complemented by voluntary slaughters of animals and, to a limited extent, market exchange of animals for agricultural foodstuffs. Commercial production systems, on the other hand, adapt their production cycle to seasonal forage availability and overcome income shortages during dry seasons by using capital that is accumulated through sales in wet seasons (Gill, 1991). In the previous section it has been shown that livestock-poor households lack sufficient animals to successfully adopt the latter mode of production. Due to the inadequate food supply from their herds, poor households may nevertheless be forced to increasingly rely on livestock sales in order to cover subsistence requirements. Situations may occur where producers find themselves selling off their breeding stock simply to feed their families, thus seriously undermining household viability (Mace & Houston, 1989; Moris, 1991). Furthermore, livestock losses in recurrent dry seasons or disease outbreaks exacerbate the marginality of small-scale operations (Roth & Fratkin, 1991). Such operations may get trapped in a vicious cycle by declining herds that are too small to meet household requirements.

An important question to ask, therefore, is how could small-scale producers increase the output of milk and surplus animals for home consumption, trade, and exchange in order to enhance the viability of their operations. One approach to improving household self-sustenance is to support small-scale producers in their attempt to rely on smallstock. In the past, a variant of this policy has been adopted by Oxfam for herd reconstitution among pastoralists in northern Kenya (Moris, 1991). The approach was to supply each recipient household with a nucleus herd of small ruminants presumed to be sufficient for each family's continued livelihood.

The case for concentrating on sheep and goats to support poor households under the changing socioeconomic and environmental circumstances rests upon several arguments. Firstly, the material reviewed in the previous section suggests that the "smallstock strategy" (Grandin et al., 1994) observed among Rendille and Maasai is probably one of the most efficient strategies for poor households to generate cash-income, rebuild their herds, and as a means to acquire large stock. The findings reported by Mace (1990) are a strong evidence that investing in smallstock is indeed the most appropriate strategy to maximize household survival chances at low herd sizes. Although, living off smallstock alone is considered to be a very risky 'boom or bust' short-term strategy that should only be followed as long as smallstock herd sizes are below a critical threshold above which an exchange of smallstock for camels becomes feasible (Mace & Houston, 1989; Mace, 1990).

Secondly, sheep and goats confer an advantage in terms of food security to small-scale producers. In sheep and goats, drought mortality rates are lower than in cattle, and post-drought herd recovery is much faster than in cattle and camels. Particularly goats may also play a crucial role in balancing year-round supply with milk for subsistence due to their ability to lactate during dry seasons, when for instance cattle produce little or no milk at all (Schwartz & Schwartz, 1985).

Thirdly, poor households tend to curtail their seasonal movements, and choose to settle around permanent water sources or trading centres. As has already been mentioned, the increasing concentration of people and stock leads to a reduction and degradation in pasture in the vicinity of permanent settlements. Due to their feeding behaviour, goats, and to lesser extent, sheep, are well suited to exploit the feed resources available under these circumstances (Lancelot et al., 1995).

A final reason why the focus on smallstock seems to be appropriate for poor households relates to the production economics of pastoral operations. Traditional pastoral herd management methods: herding, watering livestock, and milking are all labour intensive (Behnke, 1983; Grandin, 1989). Sheep and goats, however, require less labour than do cattle and camels per livestock unit (DeVries & Pelant, 1987). Smallstock holdings thus do not compromise the labour force required for the management of large stock. Also, the capital cost of the animals themselves, and consequently the economic loss incurred when an animal dies, is relatively small with sheep and goats (Johnson et al., 1986).

In order to enhance the viability of poor pastoral households, simply increasing the size of small ruminant flocks through restocking projects does not seem to be a satisfactory approach. Although they have an important redistributional advantage, herd reconstitution through donations alone will not alleviate the constraints which undermine the long-term viability of small-scale operations. In the long-run, self-sustenance of households will depend upon achieving levels of herd growth adequate to provide enough surplus animals for subsistence, market exchange, and herd accumulation. This calls for an improvement of two main traits of flock performance: reproduction and survival. These traits determine the rate of increase

and hence the sustainable offtake from the flock (Upton, 1989).

On the other hand, land, grazing and water resources are replacing labour as the limiting factor on economic activity in pastoral systems, due to population growth and increased competition for resources from other land uses (Swift, 1982). Development interventions aimed at improving (or merely maintaining) the livelihood of pastoral people and to checking the risk of environmental degradation must therefore seek to promote an increase in the physical output per animal in terms of milk, meat and other goods. In summary, with respect to the advocated smallstock strategy, an ideal intervention would, at the same time, contribute to significant improvements in herd growth and in the productive performance of pastoral sheep and goat flocks.

Before discussing potential interventions towards these goals, an important consideration needs to be kept in mind. It relates to the existing trade-off between the production of replenishable goods, i.e. milk, and surplus animals for sale, consumption, exchange and accumulation. The production of surplus animals in good condition requires that sufficient milk is allocated to lambs and kids (Ruvuna et al., 1988). Survival rates and growth performance of young stock are generally depressed under traditional pastoral management when substantial amounts of the milk produced are extracted for human consumption (Field et al., 1984). In order to maximize the net reproductive rate of pastoral sheep and goat herds and, ultimately, the potential offtake rate, most, if not all, of the subsistence milk production would have to be foregone. This might in turn affect the distinctive property of smallstock as a buffer against insecurities and imbalances in food supply, and must therefore be taken into account in evaluating specific recommendations.

Measures to improve small ruminant flock productivity

Under semi-arid environmental conditions, the main factor influencing the productivity of small ruminant flocks is climatic seasonality. Seasonal changes in temperature and moisture availability affect animal production not only by influencing the quantity and quality of available nutrients, but also by affecting the dynamics of parasitic organisms and the incidence of infectious diseases (Carles, 1985). Several studies of pastoral production systems in Kenya have found high pre-weaning mortality in sheep and goats caused by infectious diseases to be a major constraint on flock productivity in traditional management systems (Carles, 1986; de Leeuw et al., 1991; Wilson et al., 1985). The diseases afflicting small ruminants are respiratory, such as contagious caprine pleuropneumonia (CCPP), tick-borne, and brucellosis. Gastro-intestinal parasites appear to be a major health problem affecting productive performance in sheep and goats under the semi-arid conditions in northern Kenya (Field et al., 1984). Excessive helminth parasite loads are critical particularly at stages in the productive cycle when physiological requirements of animals are highest, such as during late pregnancy, lactation, and early growth period of weaned kids and lambs.

Principally, significant improvements in survival rates, productive performance (milking and growth performance), and thus flock productivity can be achieved by applying a health programme which includes vaccinations against infectious diseases, anthelmintic treatments, tick control and mineral supplementation (Wilson, 1984). Such interventions, however, are costly and need close and constant supervision. The effectiveness of health care measures in improving productivity is also likely to be reduced by the restricted and erratic supply of nutrients. In addition to its immediate effect upon survival, growth, and lactation, insufficient nutrition lowers the resistance of animals to pathological agents (Carles, 1983; Lebbie et al., 1996).

In a study conducted under semi-arid conditions in Mali, Ba et al. (1996) found that inspite of vaccinations against infectious diseases (Pasteurellosis, Anthrax, Petite Peste des Ruminants) and deworming against nematodes 50% of the kids died due to infections. The treatments had no effect on kid survival or growth until after weaning at 5 months of age. Since about 40% of kids died of malnutrition, injuries and predation losses, this study shows that first priority in reducing kid mortality should be given to improving management practices. The authors concluded that the impact of the veterinary package was limited to a small increase in flock sizes, due to a positive effect of deworming on adult goat survival. However, the costs of anthelmintics prohibit their introduction as regular deworming treatments.

Research on nomadic pastoral goat herds in Marsabit District of northern Kenya, provide some evidence that the impact of eliminating pathogenic effects on the incidence of morbidity and mortality is limited and highly dependent upon environmental conditions (Carles et al., 1984; Carles, 1986; Schwartz, 1988). In a year with above-average rainfall, treating goats with anthelmintics led to a slight increase in kid survival, but had no appreciable effect on mortality of adult animals. The anthelmintic treatment increased milk yields during and shortly after the rainy season; due to the low availability and quality of feed, however, this effect vanished during the dry season (Schwartz, 1988). By contrast, in the second year of the experiment, when rainfall was below average and the health care programme was extended to include vaccinations against CCPP and

Brucellosis, tick control measures as well as mineral supplementation, herd productivity fell drastically in both the control and the treatment flocks due to inadequate nutrition. Yet, a substantial interaction occurred between health care measures and feed availability such that the reduction in productivity in the treated herd was more than twice as high as that in the control herd. These results suggested that health care measures, especially anthelmintic treatments, improved pastoral goat herd productivity only when feed availability was not constraining animal performance (Schwartz, 1988).

The scope for alleviating restrictions imposed on animal performance by the seasonally and annually varying supply of nutrients is very limited, especially under the changing socioeconomic and environmental conditions outlined above. Given the erratic nature of primary production in semi-arid areas, the pastoral producer lacks the ability to exert direct control over future biological states of the grazing system, and thus to manipulate his forage supplies. The basic problem of matching feed supply and demand is overcome by adaptive management, of which the most prominent form is the movement of animals onto pastures with adequate forage (Behnke, 1994). However, the distinctive advantage derived from herd mobility for balancing nutrient shortages is lost in the transition to sedentariness, and this introduces an additional constraint on animal productivity. In this situation, intensifying land use by adopting forage production and/or forage conservation are potential options for synchronising feed supply and demand, especially during the dry season. Successful forage cultivation is feasible only on high potential land within the grazing system, particularly on the scarce dry season pastures. Production and conservation of forage are very labour intensive, and this represents a serious limitation to pastoral households considering these activities as a way of improving their feed resources. Also, forage interventions may be difficult to implement under communal grazing tenure (Bekure & de Leeuw, 1991; Coppock, 1994).

Alternatives to herd mobility as the most efficient form of adaptive management to overcome nutritional deficits are few. One strategy is to manipulate the total seasonal nutrient requirements of the herd, instead of attempting to improve the supply side of the nutrient balance. Adapting total forage demand of livestock herds to feed availability is essentially what Sandford (1982) has called an "opportunistic strategy". The main idea is to adjust the number of stock up or down in response to variation in forage resources. In his paper, Sandford discussed opportunism as a management strategy to cope with inter-year variability in primary productivity of the grazing system, but opportunism could as well be used as an adjustment to inter-seasonal fluctuations in forage supply. Irrespective of time scale, the practicability of the opportunistic strategy hinges upon access to livestock markets to dispose of surplus stock, and on sufficient market demand to capture the implied increases in flow without a collapse in prices (Sandford, 1982). Difficulties relating to both factors have been shown to hamper market sales by pastoralists during dry seasons in northern Kenya (Schwartz, 1986), Maasailand (Bekure & de Leeuw, 1991), and southern Ethiopia (Coppock, 1994). Although the same studies found that forced and voluntary slaughters of stock generally peaked during dry seasons or droughts, the authors argue that substantial increases in market sales would be needed to achieve a balance between the nutrient requirements of the herds and pasture forage production.

Proposed intervention

Nevertheless, the adjustment of stock numbers could be complemented with an additional measure geared towards manipulating total seasonal nutrient requirements of the herd, namely the confinement of breeding to one or several selected periods of time in a year. Continuous breeding throughout the year is typical for pastoral sheep and goat flocks in Kenya, an important exception being Maasai producers in Kajiado District who attempt to control breeding of their smallstock using breeding aprons (de Leeuw & Peacock, 1982; de Leeuw et al., 1991). Continuous breeding is possible due to the ability of local sheep and goat breeds to reproduce year round. The principal advantage of an aseasonal breeding regime is a continuous supply (although in seasonally varying proportions) of milk, meat and surplus animals to pastoral households, and the low input of labour and management required. Yet, this strategy produces low milk yields, kid survival and growth whenever late pregnancy and birth fall into periods with suboptimal forage availability (Mellado, et al., 1996; Wilson et al., 1985). Moreover conception rate, prolificacy and kidding rates are compromised whenever mating occurs under poor nutritional conditions (Delgadillo & Malpaux, 1996; Walkden-Brown & Restall, 1996). In sum, an aseasonal breeding regime implies that nutrient requirements of the flock remain relatively constant over the year; due to variation in pasture growth, this leads to both wastage and deficiencies (Carles, 1983).

The control of reproduction might allow the grouping of stages in the productive cycle with critical nutritional requirements during the limited periods in which these requirements can be covered by the forage produced. Although it would be necessary to split up herds in several management units, and thus increase labour demands for herding, watering, and breeding management, significant economies of scale are likely to be achieved from creating more homogenous groups of animals. For example, guarding lambs and kids around the homestead would be limited to certain periods in a year, thus saving labour for other tasks (de

Leeuw et al., 1991). In addition, management practices such as castration and vaccination would be carried out more efficiently, since they would be performed on a larger number of animals on a few occasions only.

However, past experience with development interventions aimed at altering existing pastoral techniques of livestock and rangeland management indicate that due attention has to be payed to key features of these systems, among which uncertainty in production conditions and its effects on pastoral households is probably the most pervasive and serious one (Ellis & Swift, 1988; Mace & Houston, 1989; Southey, 1992). Intra-seasonal and inter-year variations of climate result in uneveness in resource requirements and the flow of output of livestock herds. Decision rationality dictates that pastoral producer's behaviour and decision making are not invariant to the perception of this production risk. Consequently, situations may arise in which some of the various shortfall minimizing pratices developed by traditional herdsmen are incompatible with the adoption of a seasonal breeding strategy. For instance, limiting reproductive activity in smallstock herds to a short period in a year implies a once a year reproductive schedule, such that all outputs will also tend to be produced over a short period of time. Inadequate rainfall during stages of the production cycle with high nutrient requirements, i.e., from late gestation until weaning, may precipitate high rates of reproductive wastage, poor survival of both breeding animals and youngstock, and low milk output from the herd. Hence, such uncertain events may result in a considerable loss of production and may undermine the survivability of pastoral households and their smallstock herds. Also, the once-a-year pulse of output asssociated with a seasonal breeding strategy may conflict with the role of smallstock as a buffer against insecurities and imbalances in food supply. It could be argued that an aseasonal breeding strategy is better suited to ameliorate the effects of uncertainty and to produce a more constant flow of goods, although at the cost of a somewhat lower long-term average herd productivity.

Current state of knowledge

The restriction of breeding as a management strategy to match nutrient demands in pastoral sheep and goat flocks with seasonal feed supplies has so far received little attention in research, although it is often considered to be an important step in improving small ruminant productivity (Carles, 1983; Field, 1984; Bradford & Berger, 1988; Delgadillo, 1996). From observations made on Rendille goat herds, Carles (1986) concluded that birth, just before or just after a rainy period (defined as a six-week period receiving measurable rainfall), resulted in the highest growth rates in kids. However, no account of environmental influences on conception and birth rate, litter size, kid survival or lactation yields was given. In a simulation study, Smith et al. (1982) used the same data to determine the optimum seasons for kidding with regard to milk yield and kid survival. Based on a single-animal simulation of a two-year old Small East African doe, kidding in October at the onset of the short rainy season was found to result in the highest milk yield, kid survival and growth rate.

The most detailed assessment of the impact of seasonality on pastoral sheep and goat flocks is that of Wilson et al. (1983, 1984, 1985). This study was conducted on a Maasai group ranch in Kajiado District, Kenya, and revealed a marked effect of the season of birth (short rains, short dry, long rains, long dry) on survival and growth rates in lambs and kids until weaning. Although some differences in reproductive performance, as determined by litter size and parturition interval, were observed between seasons of birth, the results were inconclusive with regard to the factors which may have influenced these two traits. This was due to the observational nature of the study: breeding was actually not controlled experimentally. Since only the date of birth and not the time at which females were re-bred after giving birth was recorded, the reported estimates of parturition intervals are unlikely to be free of error (see Upton (1989) for an account of problems associated with defining and estimating parturition intervals).

Due to the non-experimental nature of the study, inferences concerning the effect of environmental conditions at the time of mating upon key parameters determining reproductive performance such as conception, birth and prolificacy rates could not be drawn. Indeed, the finding that the highest productivity in Maasai sheep and goat flocks (measured as total live weight (kg) weaned per dam post-partum weight (kg) and year) is achieved when births occur during the short dry season (see Wilson et al., 1985) conflicts with that of de Leeuw et al. (1991), which suggest that restricting breeding might have caused poor reproductive performances in Maasai group ranches. The latter authors argue that restricting breeding to a 3-4 month period beginning at the onset of the long dry season leads to high flock productivities only if, prior to the mating season, good rains, or the movement of flocks to pastures with adequate forage ensure high conception rates.

It is difficult to assess from the above information if controlled breeding is indeed an effective strategy for alleviating the constraints imposed by seasonal nutrient shortages. And in the light of the limited options available for improving livestock production in pastoral systems, it is important to increase our understanding of the potential benefits and pitfalls associated with controlled breeding as a management strategy.

Methodological issues

In studying the effects of seasonal breeding on biological productivity of pastoral goat herds two aspects deserve special attention. Firstly, seasonality is a composite of a number of environmental effects that have not only an impact upon, in the short term, performance parameters of goat herds, but also exert a sequential influence over the entire production cycle. Therefore, in studying the effect of a restricted breeding regime on herd productivity, it is important to extend herd recording, at least from the time at mating, until the time of disposal of young stock. In the presence of large, climatically induced variations in production conditions between both years and seasons, studies of controlled breeding should be designed to cover at least two complete productive cycles in different years, whereas the treatments should consist of several consecutive seasonal "breeding groups" in which breeding is confined to a fixed period of time. Both aspects of experimental design require setting up several experimental groups of animals which need close supervision and management. These conditions are essential to achieving an acceptable degree of comparability and are generally difficult to meet in traditionally-owned pastoral herds. The particular role of experimentation is emphasized here because a large proportion of previous reports on the effects of seasonality on African pastoral goat herds were purely retrospective in nature, such as that of Wilson et al. (1983, 1984, 1985) mentioned above. Testing specific hypothesis with data that were collected in observational or survey-type studies tends to be problematic, because, often, the set of data to be analysed was not, or not optimally designed for this purpose. With such data, influences that are not under the control of the investigator are almost always present and acting on the study objects. The main problem is that in the presence of confounding influences, it is logically not possible to attribute causality to perceived differences between measured variables (Underwood, 1996). This is confirmed by the study of Wilson et al. (1983, 1984, 1985) who found that the most general influence on productivity of sheep and goats was exerted by flock ownership. Although differences and relations between measured variables may be detected in observational studies, their interpretation is problematic and requires caution (Hurlbert, 1984; Jager & Looman, 1995).

Secondly, productivity assessments at the flock level that incorporate all outputs (meat, milk etc.) should be used to compare levels of technical efficiency achieved in flocks mated in different seasons. Available efficiency indices and their suitability for productivity assessments in small ruminant production systems have recently been reviewed by Bosman et al. (1997). These indices typically relate gross output in terms of monetary value, mass or energy to the number of animals (or their total liveweight, or metabolic liveweight) required to produce it. The majority of the available measures of efficiency is geared towards single output meat systems, and therefore are, at best, only suited for evaluating isolated factors contributing to overall flock productivity, such as reproductive performance of breeding females. Although Bosman et al. (1997) discuss various fallacies and drawbacks associated with the individual approaches, they fail to address two more fundamental aspects which, when ignored in computing efficiency measures, can lead to questionable results in livestock herd productivity assessments. These relate to the effect of population structure and population dynamics upon the calculation of efficiency measures.

Neglecting for the moment effects of genetic and environmental origin, performance traits such as the probability of conceiving, survival, litter size, milk yield and liveweight gain are undoubtedly a function of the stage (e.g., age, parity number, age within parity number, or another biologically meaningfull categorization) an animal has reached in its species specific life-cycle. For example, it is well established that fecundity in breeding does increases almost linearly with parity number, whereas the amount of milk produced increases curvilinearly with the number of lactations (Raats et al., 1982; Devendra & Burns, 1983). Consequently, these changes in performance over successive life-cycle stages must affect the computation of productivity measures whenever the stage classes are not represented in equal proportions in the sample data. Irrespective of the type of index used, i.e. reproductive, productive or flock performance, the bias introduced by unequal stage abundances in a herd can be controlled for by requiring the underlying distribution to be stationary, i.e. relative numbers of individuals in each stage do not change over time (Putt et al., 1987). If no adjustment is made for such a stable herd or flock structure, comparisons between different breeds or between flocks of the same breed under different environments, treatments, or management systems made on the basis of productivity indices are likely to lead to invalid inferences. Also, as has been pointed out by Upton (1989,1993) and Baptist (1988, 1992a), evaluations of this kind are only valid if carried out under 'standard conditions' with respect to herd growth and size. Allowance has to be made for breeding flock replacements in order to avoid comparing flocks which grow at different rates. This problem may be resolved by keeping herd size constant and considering the differences in productivity between each case that could be achieved subject to this constraint (Upton, 1989).

Available efficiency measures for productivity assessments at the flock or herd level do not correct for the bias introduced by differences in population structure. The denominator of the respective output/input ratios are usually calculated as averages over all life-cycle stages, such that all individuals are treated as identical. Peacock (1987) argues that using the mean weight of the flock as denominator can serve as a representation

of the demographic structure of the flock. However, whether liveweight alone can serve as a predictor of an individual's future survival, growth and fecundity is questionable, and the problem that demographic stability is implicitly assumed still prevails with this approach. Similar arguments hold with respect to the effect of herd growth upon the calculation of productivity indices. Although attempts have been made to allow for overall net inventory changes (e.g. Peacock's (1987) flock productivity index), this cannot be regarded as an appropriate representation of the underlying population dynamics, since accurate assessments of inventory changes must be based on estimates of changes in animal numbers in each stage class and sex cohort (Upton, 1989).

Several approaches based on herd growth modelling techniques have recently been developed to overcome the shortcomings of conventional productivity measures. The use of a so-called steady-state herd model along with an appropriate measure of technical efficiency, e.g., total output produced (measured in monetary or energetic terms) per unit feed energy requirement when the population is in a steady-state with respect to population dynamics, has been advocated by Baptist (1992a), James and Carles (1996), and Upton (1989, 1993) for making standardised comparisons. With a steady-state herd model, the stable structure of a livestock herd is computed for a specified set of stage and sex specific survival and fecundity parameters. In order to maintain herd size constant over time, a culling regime has to be imposed, which in its simplest form consists of culling at a pre-specified age all female and male surplus animals not needed as breeding stock replacements. The productivity index itself is then, for example, computed by dividing the sum of the value of all outputs (milk, meat, etc.) by total feed-energy requirements of the herd at equilibrium.

The techniques that have been developed so far for assessing herd productivity at the steady-state are based on an age-classified approach of modelling herd dynamics over time. Although classifying individuals in a population by age cohorts is the the most straightforward and widely used classification, age-structured population models implicitly assume that properties other than age are irrelevant to an individual's demographic fate. From this is follows that if vital rates (i.e. rates of survival, growth, and reproduction) also depend on factors other than chronological age, these must either be highly correlated with age or the distribution of individuals among the relevant categories must be stable. However, as indicated above the demography of domestic livestock species may depend on size or developmental stage much more than on age (e.g., parity or size), and often these variables are only weakly correlated with age. Situations may also occur in which the age of individual animals is difficult to determine accurately, but other characteristics such as body size, reproductive status, or parity number may be more convenient to measure and more pertinent to questions relating to population dynamics.

A further restriction of currently available methods for steady-state herd productivity assessments (Baptist, 1992a; James & Carles, 1996) are that they allow for only a broad categorization of the different types of animals in a herd into a rather limited number of classes. Additionally, within these categories performance traits cannot be made dependent upon the age an animal has reached in its species-specific life-cycle. Especially vital parameters and performance traits pertaining to breeding females such as fecundity, litter size, milk yield, liveweight and liveweight gain are assumed to remain constant throughout their productive lifespan. The methods proposed by Baptist (1992a) and James and Carles (1996) also impose restrictions, to varying degrees, upon the specification of survival rates. The approach of James and Carles (1996), which has been implemented in a computer program, LPEC (PAN Livestock Services, 1991), assumes constant survival rates in each animal class, irrespective of age. The computer program (PRY) developed by Baptist (1992a) is somewhat more flexible in this respect, but it still assumes, for instance, that the same survival rates apply to surplus and breeding females in a herd, as well as to reproductively active and (temporarily) infertile breeding females.

These limitations can have profound impacts upon the determination of herd dynamics, herd structure at the steady-state, and hence optimal offtake rates and productivity. In order to refine the concept of steady-state herd productivity assessment and improve its flexibility and applicability, it therefore appears worthwhile to explore alternative methods of modelling herd dynamics over time and of deriving optimal steady-state herd structure and offtake rates.

1.3 Objectives and structure of the thesis

In view of the limited information available on the effect of seasonality upon small ruminant productivity in semi-arid areas, as well as on the advantages and disadvantages associated with a controlled breeding regime, a systematic breeding programme in a herd of Small East African (SEA) goats was initiated for a period of three years (1984-1987) at the Ngare Ndare research station of the University of Nairobi in Isiolo District, northern Kenya (Schwartz & Carles, 1987). Part of the data collected in this experiment has already been published in a series of papers reporting either preliminary results (Rutagwenda et al., 1985; Schwartz &

Carles, 1987), or investigating factors affecting kid mortality (Gachuiri et al., 1986) and milk yields (Wahome et al., 1994) of SEA goats under semi-arid conditions in northern Kenya. However, a detailed statistical analysis of these data covering all parameters relevant to assessing overall flock productivity has not yet been undertaken. Similarly, a systematic investigation of the effects of the implemented controlled seasonal breeding regime on overall performance of experimental flocks is not yet available.

Using this set of data, the present study was undertaken to (1) assess the effect of a seasonal breeding regime on various traits determining biological performance of pastoral goat flocks, and (2), to test the hypothesis that there is an optimal period in a year to which breeding can be restricted to improve overall biological flock productivity. However, the foregoing section made clear that the adoption of the latter hypothesis may be considered a necessary, but not sufficient condition to prove the superiority of controlled versus uncontrolled breeding. In particular, it will be necessary to address the question whether, in biological terms, restricting reproductive activity in pastoral goat herds to a single short mating season at a particular time of year entails a significant increase in production risk. Also, the distinctive role of goats in buffering insecurities and imbalances in food supply to pastoral households needs to be taken into account. In this end, goats traditionally are reared for dual-purpose meat and milk production. Nevertheless, the transition towards a more sedentary life-style is likely to increase the pressure on pastoral producers to specialise and commercialise their mode of production. It is therefore interesting to test the hypothesis whether different optimum breeding periods can be identified for a dual purpose meat and milk production and for a single purpose meat production.

This thesis is structured in 8 chapters. With the exception of the present and the final chapter, all other parts (Chapter 2 through 7) were written with the intention to be self-contained and to stand on their own as independent papers. Chapters 2 to 5 will be devoted to the statistical analysis and interpretation of the effects of six different, seasonally restricted breeding regimes on, respectively: reproductive performance traits; survival rates of kids and does; growth performance of kids and body weight development of does; and milk production. As the first paper in this series, the materials and methods section of Chapter 2 provides a detailed description of the study area and study design

In Chapter 6 an extension to available methods of steady-state herd productivity assessment and modelling will be developed. It will be based on a stage-structured matrix population model and use non-linear mathematical programming to derive optimal herd structure and stage-specific offtake rates. Estimates of traits of reproductive and productive performance, as well as of survival obtained from the statistical analyses of the experimental data presented in preceeding chapters will be used in Chapter 7 to parameterise the proposed productivity assessment model for six different breeding seasons and an aseasonal reference group. This modelling exercise is carried out in order to test the formulated hypotheses concerning the effects of seasonal breeding on the biological performance of pastoral goat flocks. Finally, Chapter 8 provides a summary and a general discussion of the main themes and results of this work.

Chapter 2

Effects of controlled seasonal breeding on reproductive performance traits of pastoral goat herds in northern Kenya

2.1 Introduction

In African pastoral systems, poor and fluctuating nutritional levels can cause reproductive inefficiencies in goat flocks. Despite the ability of many local goat breeds such as the Small East African to be non-seasonal, breeding females may exhibit prolonged periods of anovulation or anoestrus, reduced ovulation rates, as well as high embryonic and perinatal losses as a result of poor nutrition (Delgadillo & Malpaux, 1996; Walkden-Brown & Restall, 1996). Traditionally, pastoral producers in northern Kenya exert very little control over reproductive activity in their goat herds. In these systems, the impact of variations in pasture growth and forage quality on reproductive and other aspects of herd performance is minimized by optimizing migratory pathways between quality patches (Western & Finch, 1986). However, the increasing human demographic pressure on semi-arid rangelands in Kenya as well as a number of profound changes in the socioeconomic environment that have occurred over the last decades have triggered a rapid decrease in the mobility of pastoral herds and settlements (Schwartz & Schwartz, 1985; Hogg, 1986; Bennett, 1988). Also, the occurrence of sedentary pastoralism in the vicinity of small towns and trading centres is often characterised by a gradual commercialisation of pastoral production (Roth, 1990; Roth & Fratkin, 1991).

With respect to pastoral livestock production, the main problems arising from these developments are that the impact of climatic seasonality on all aspects of herd performance will tend to be aggravated. At the same time, improvements in the efficiency with which scarce rangeland resources are used are urgently needed to support an increasing human population. However, due to the low and erratic supply of nutrients from semi-arid rangelands it is difficult to envisage alternatives to herd mobility for overcoming seasonal nutritional deficiencies. One possible management intervention for achieving a better balance between nutrient requirements and supply in pastoral livestock operations is to concentrate reproductive activity in a single short breeding period. Restricting mating to a time that synchronizes the most physiologically demanding phases of the reproductive cycle with peak pasture production has been argued to be an important step to improve the productivity of pastoral goat herds in northern Kenya in particular (Field et al., 1984), as well as of small ruminant herds in tropical regions in general (Carles, 1983; Bradford & Berger, 1988; Delagadillo & Malpaux, 1996). Nevertheless, detailed information on the effects of controlled seasonal breeding on reproductive performance of goats in semi-arid regions in Africa is currently not available. Additionally, the few published results on this subject were obtained mainly from observational studies (e.g., Wilson et al., 1984; Wilson & Traoré, 1988) and there is a clear lack of experimental tests of the effects of such a management intervention on various reproductive traits, including probabilities of conception and abortion, as well as of rates of fertility, prolificacy, fecundity, and the proportion of kids weaned. Data on these parameters are indispensable for a sound assessment of how a controlled breeding regime affects biological (technical) efficiency of pastoral goat herds.

The objective of this study is to examine the effects of a restricting breeding regime on reproductive traits of Small East African (SEA) goats maintained under pastoral management on a semi-arid thornbush-savannah in northern Kenya. The effects of such a management intervention are evaluated by dividing the year into six consecutive mating seasons each of two months duration, so that the impacts of within-year variations in forage supply and production conditions are explicitly taken into account. This range of mating periods is intended to allow the identification of the most favourable period to which breeding could be restricted in this region to achieve optimal reproductive performance.

2.2 Materials and Methods

Study area

Data for this study were part of an experiment conducted at the University of Nairobi's Ngare Ndare research station in the Isiolo District of northern Kenya. The research station is situated on a former holding ground of

the Livestock Marketing Division, Ministry of Agriculture and Livestock Development, approximately 18 km southwest of Isiolo township, on the northern foothills of Mt. Kenya (centerpoint 0°22'N, 37°26'E). According to Ojany and Ogendo (1973), the climate in northeastern Kenya can be classified as tropical continental, semi-desert type. Rainfall in the study area is distributed over two distinct rainy seasons which receive 75 percent of total annual rainfall, a long rainy season from March to May, and a short rainy season from October to November. Rainfall records taken at the nearest meteorological station in Isiolo township display a long-term annual average of 615 mm (Kenya Meteorological Department, 1931-1991, n=49). The long-term median annual rainfall is 583 mm; in 50 percent of the years rainfall amounts ranged between 498 and 694 mm.

The predominant vegetation type is open *Acacia tortilis-Lippia carviodora* dwarf shrub bushland (Cornelius & Schultka, 1997; Schultka & Cornelius, 1997), occurring on upland sites, valley slopes and valley bottoms. On heavily grazed pastures in these areas, the herblayer is characterized by high frequencies and coverages of the grasses *Sporobolus nervosus* and *Tragus bertorianus* while the dominant dwarf shrub is *Indigofera spinosa*. *Chrysopogon plumulosus* and *Hibiscus micranthus* dominated communities are found in transition areas between uplands and riparian zones. Both of these communities are important forage resources for livestock (Walsh et al., 1993). *Acacia mellifera-Acacia paolii* shrublands are associated with deeply layered Vertisols on upland sites and valley bottoms. The dominant grasses are *Setaria acromelena and Cyperus blysmoides*, while *Farsetia stenoptera* and *Blepharis linnarifolia* are characteristic forb species occurring on these sites. *Acacia reficiens* and *Acacia horrida* thickets are confined to sites on eroded Vertisols in valley bottoms. *Acacia xanthophloea* or *Acacia tortilis* riparian gallery forests and woodlands occur in areas with permanent ground water access. Seasonally flooded plains are dominated by semi-terrestric *Cynodon plectostachyous* swards and are frequently grazed during dry seasons. According to the classification of Pratt and Gwynne (1977) the research area falls into ecozone V.

Experimental design

The study commenced in early 1983, when a herd of Small East African goats comprising approximately 60 mature and immature females was provided by the Research Division of the Ministry of Livestock Development. By culling unsuitable animals and further local purchases, a total of 90 mature does and 50 immature females were available at the end of 1983. This herd was used to start a systematic breeding programme designed to achieve year-round mating, kidding, and weaning. Experimental animals were between one to six years of age. Female replacements required at later stages of the study were obtained from immatures born during the course of the experiment. The female herd was stratified according to age and body weight, and animals assigned to treatment groups were randomly sampled from each stratum. Females weighing less than 20 kg were excluded from the sampling procedure. Each treatment group comprised approximately 18 does.

In this experiment the treatment structure consisted of a sequence of 18 treatment groups, into each of which a buck was introduced for a period of two months. At the end of each two-month period the buck was transferred to the next group, so that the experiment generated six different treatment groups per year. Hereafter, the latter will be referred to as the "breeding groups" of the experiment. The first breeding group was set up at the end of January 1984, and the breeding programme was concluded in January 1988, ending with breeding group number 18. Thus, three complete productive cycles were obtained for each two-month breeding group over the four years of the experiment. Summary information on the number of breeding females and number of kids born in the first seventeen breeding groups is displayed in Table 2.1.

For the purpose of analysis, breeding group eighteen was discarded because of incomplete records. The three replications for each breeding group were labelled with an identifier, *mating season*, which was used as the treatment variable in subsequent analyses. Except for mating seasons 4 and 5, all treatment levels refer to a breeding season of two months length. Due to a delay which occurred in setting up breeding group 4 in 1984, breeding in mating seasons 4 and 5 were assumed to have taken place over a 3 month period (Table 2.1). For the same reason, mating season 6 was not observed in the first year of the experiment, and only two complete reproductive cycles were available for that group. Note that the experimental design did not include a control group in which does were allowed to breed continuously throughout the year for the entire experimental period. Therefore, no "aseasonal" mating group was available as a reference for comparative purposes.

A total of 145 does were utilized to set up the 17 breeding groups. From these, 93 animals were allocated to two or more different breeding groups in the course of the experiment. A total of 65 does were observed in at least two consecutive production cycles within the same mating season group. Thus, with regard to the statistical analysis of the experimental data, individual does were nested within the observed combinations of mating season×production cycle.

Table 2.1. Summary information on breeding and mating season groups

Mating season [number]	Breeding group	Year of the experiment	Number of does joined	Number of kids born
February-March	1	1984	19	30
[1]	6	1985	17	20
	12	1986	17	22
April-May	2	1984	18	19
[2]	7	1985	17	16
	13	1986	17	14
June-July	3	1984	17	14
[3]	8	1985	18	21
	14	1986	14	23
August-October	4	1984	18	11
[4]	9	1985	18	31
	15	1986	18	26
October-December	5	1984	17	17
[5]	10	1985	14	13
	16	1986	12	14
December-January	-	1984	-	-
	11	1985	18	24
[6]	17	1986	18	16
Total			145 (287)*	331

* 93 does were allocated to more than one breeding group during the course of the experiment.

Herd management and data collection

The animals were maintained under traditional management, and all day-to-day herding decisions were left to local pastoralists. The goats were herded every day from 07:00h and brought back to the station for watering at 12:00h. Afternoon grazing started at 15:00h and ended at 18:00h, when the animals returned to night enclosure. During a grazing day the animals walked between 5 and 10km, where longer distances were travelled during the dry season.

Newborn kids were weighed and ear-tagged as soon as possible after birth. All male kids were castrated within the first week of life using the rubber ring method. Until approximately two months of age kids were kept for the whole day in the night enclosure, and thereafter until weaning at 16 weeks of age were left to roam freely in immediate vicinity of the night enclosure. Kids were allowed to suckle their dams from their return from afternoon grazing until the next morning; does were not milked during lactation except for milk yield measurements. Surplus young stock were disposed of at one year of age. All female kids were allocated to the breeding herd at one year of age, with the exception of those culled for poor conformation.

In order to minimise the effects of infectious diseases and internal parasites on animal performance, a health care programme was carried out regularly in the experimental herd. The animals were drenched twice a year with Panacur® (Fenbendazole, Hoechst AG, Frankfurt a.M.) prior to the rainy seasons and were vaccinated once a year against Contagious Caprine Pleuro-Pneumonia (CCPP), which is prevalent in the area. Whenever tick infestation was noted, the animals were sprayed with Bacdip® (Organophosphorus, Bayer, East Africa Ltd.). A salt lick, Maclick® (KFA Ltd. Nairobi) was offered in the night enclosures, and injuries were treated with antibiotic spray.

Time in the experiment was divided into periods of two weeks, each period starting and ending on a Monday. Routine measurements of weight (kg) of all animals, milk yields (ml) were carried out at the beginning of each two-week period and entered in record sheets. All events such as abortion, birth, and death were recorded continuously. Adult animals were weighed using a weighing crate and measurements were made to the nearest 0.5 kg. Kids were weighed immediately after birth using a spring balance to the nearest 0.25 kg.

Pasture condition was judged every two weeks using a subjective phenological pasture condition score for

the herblayer (range condition score [I]), including grasses, herbs, and small dwarf shrubs. Scores ranging from 1 to 4 (low to high) were allocated at each occasion according to forage availability and quality. The condition score for the herblayer was upgraded to a maximum score value of 5 to integrate the contribution of the bush and tree layers with regard to browse availability and the production of high quality litter such as leaves, flowers and fruits (range condition score [II]). Scores of 1 to 3 generally occurred during the dry seasons, and 4 and 5 during and immediately after the rainy seasons.

Traits studied

The definition of parameters of reproductive performance was based on the recommendations of Terrill and Foote (1987). In addition to the parameters suggested by these authors (i.e., fertility, prolificacy, fecundity, and proportion weaned), conception (=*number of does pregnant per doe exposed*) and abortion rate (=*number of does aborting per doe pregnant*) also were estimated in the present study. The higher resolution with respect to the components of reproduction was meant to facilitate investigating the influence of seasonality in forage supply on compound measures of reproductive performance such as fecundity (=*number of offspring born alive or dead per doe exposed*) and proportion of kids weaned (=*number of kids weaned per doe exposed*). Birth rate was defined as the *number of does kidding (without abortions) per doe exposed* and differs from the definition of fertility reported by Terrill and Foote (1987) in that abortion events do not enter into the calculation. The same applies to prolificacy rates, which in the present study were defined as the *number of offspring born alive or dead (without abortions) per birth event*.

The control of breeding to a single breeding period dictates once-a-year reproduction. The estimation of parturition intervals has little relevance in this setting and was therefore not considered. Moreover, the number of breeding does available in the experiment precluded the estimation of the probability of rebreeding for consecutive production cycles within the same mating season group; as mentioned above, only 65 does were allocated at least twice to the same mating season treatment.

Statistical analysis

Conception, abortion, and birth rate are dichotomous outcomes and were analysed through logit models (extensive discussions of logit models can be found in Agresti (1990) and Christensen (1990)). Poisson regression models were fitted to *prolificacy*, *fecundity*, and *weaning rate*. By definition, these outcomes are rates where the measurements to be analysed are the number of events of a specified type divided by a relevant baseline measure E (Agresti, 1990) - e.g., for *prolificacy*, the number of offspring born divided by the number of does kidding. In contrast to logit models where the baseline is given by the frequency of the second outcome of the dichotomous response, an appropriate and context specific measure E (e.g., the number of does kidding) must be specified in order to properly define the rate to be modelled. The logarithm of this baseline measure, the so-called offset, enters as a constant parameter into the models being estimated.

Logit and Poisson regression models for rates and proportions are special cases of generalized linear models (GLM), a class of models first suggested by Nelder and Wedderburn (1972). An extensive treatment of these models is given by McCullagh and Nelder (1989). GLMs can be extended to *generalized linear mixed models* (GLMM) which allow for simultaneously taking into account random model effects (or dispersion components) and non-normally distributed errors. In the generalized linear mixed model approach, instead of fitting a fixed-effects model to expected outcomes, a mixed model is fitted to the *conditional* mean of the observations, given the random model effects using quasi-likelihood or pseudo-likelihood procedures (see Wolfinger & O'Connell, 1993; Littell et al., 1996).

The SAS procedure GENMOD (SAS Release 6.12, 1996) and the SAS macro GLIMMIX (October 1995 version) were used to fit fixed and mixed effects logit and poisson regression models, respectively. REML estimation was used for models containing random effects. If appropriate, best linear unbiased predictions (BLUP) of random effects were obtained through the ESTIMATE statement provided by the SAS macro GLIMMIX. The likelihood ratio statistic or *deviance* served as a criterion to test for overall agreement between modelled and observed responses and to exclude from consideration models that did not fit observed data well. In analogy to analysis of variance the deviance of a sequence of models, each including one term more than the previous one, can be used to produce an analysis of deviance (McCullagh & Nelder, 1989). Here, the change in deviance between nested models is used as a measure of discrepancy and compared to a χ^2 distribution with p degrees of freedom as a test of statistical significance, where p is the difference in degrees of freedom between two nested models.

Identification of parsimonious models for the data was based on backward selection from a model including all possible interaction terms up to the third degree, with terms sequentially removed if the reduction in deviance, adjusted for all other terms in the model, was not significant at the 15 percent level. However, the

mating season treatment effect was retained in all models, regardless of its significance, in order to provide smoothed estimates of all traits for the six mating seasons.

The three consecutive reproductive cycles were considered to be random blocked replications. Therefore, the random factor of reproductive cycle was tested for significance in all models that were developed. The treatment structure was an *n*-way factorial arrangement, *n* denoting the number of treatment and classification factors included in the analysis. The sole treatment factor considered was mating season. Classification factors evaluated in preliminary models fitted to rates of conception, abortion, prolificacy, and fecundity are listed in Table 2.2. In analysing birth rate and proportion of kids weaned, lagged median range condition scores [I] and [II] at mating were not taken into account.

Table 2.2. Classification factors used in statistical analyses.

Classification Factor	Levels	No. of observations in each level	
• Doe live weight at breeding (kg)	< 25	28	
	25to30	76	
	30to35	63	
	35to40	79	
	≥40	41	
• Parity (number of previous parturitions)	0	72	(65)*)
	1	80	(65)
	2	70	(63)
	3	43	(39)
	≥4	22	(18)
• Lagged median range condition score [I] for the period at the start of mating and the two immediately preceeding periods	1	66	
	2	66	
	3	72	
	4	83	
• Lagged median range condition score [II] for the period at the start of mating and the two immediately preceeding periods	1	17	
	2	30	
	3	49	
	4	103	
	5	88	

*) Figures in parentheses relate to observed frequencies at the onset of lactation.

Since the effect of mating season and that of lagged range condition scores [I] and [II] at mating were confounded, fitting separate models for assessing the effects of these variables was warranted to avoid estimation problems arising from multicollinearity in the linear predictor. In order to control the experimentwise error rate at the prespecified level of α=0.05 when making multiple comparisons of factor level means, both the bonferroni and Tukey multiple comparision procedures were used. The procedure giving the narrower confidence limits was then chosen to report significance probabilities of differences in factor level means. This choice is proper since it does not depend on the observed data (Neter et al., 1996).

2.3 Results

Range condition

This section provides a summary of environmental conditions prevalent during key phases of the productive cycle, as captured by the pasture condition assessment procedure described above. It is intended to facilitate interpretation of the impact of the breeding season treatment on performance traits. The biweekly values for range condition scores [I] and [II] recorded throughout the experimental period were used to compute median scores for each of the six mating season groups over a production cycle of one year duration (Figure 2.1). The graphs show the timing of mating, kidding and weaning events in relation to the average pasture condition experienced over three (mating seasons 1 to 5) and two (mating season 6) consecutive production cycles.

The most favourable pasture conditions during the breeding period were observed in mating season 2 (long rainy season) and 1 (end of short dry season). For mating groups 3 (beginning of long dry season) and 4 (middle of long dry season), the onset of mating was characterized, respectively, by rapidly deteriorating and poor forage quality and quantity. Fair range conditions prevailed during the short rainy season in November and December, when mating took place in group 5. Somewhat less favourable forage conditions where encoutered by breedong does in mating group 6 during the short dry season. The poorest range conditions at kidding were experienced by mating season group 2, in the middle of the long dry season. Similar range conditions, with respect to score [I], prevailed at the time of kidding in group 1 (beginning of long dry season). The peak in the adjusted range condition score [II] during the same period was caused by an increased availability of high quality litter such as leaves, fruits and flowers of Accacia species. According to Schultka and Schwartz (1987), these are the most important dry season browse for goats in this region.

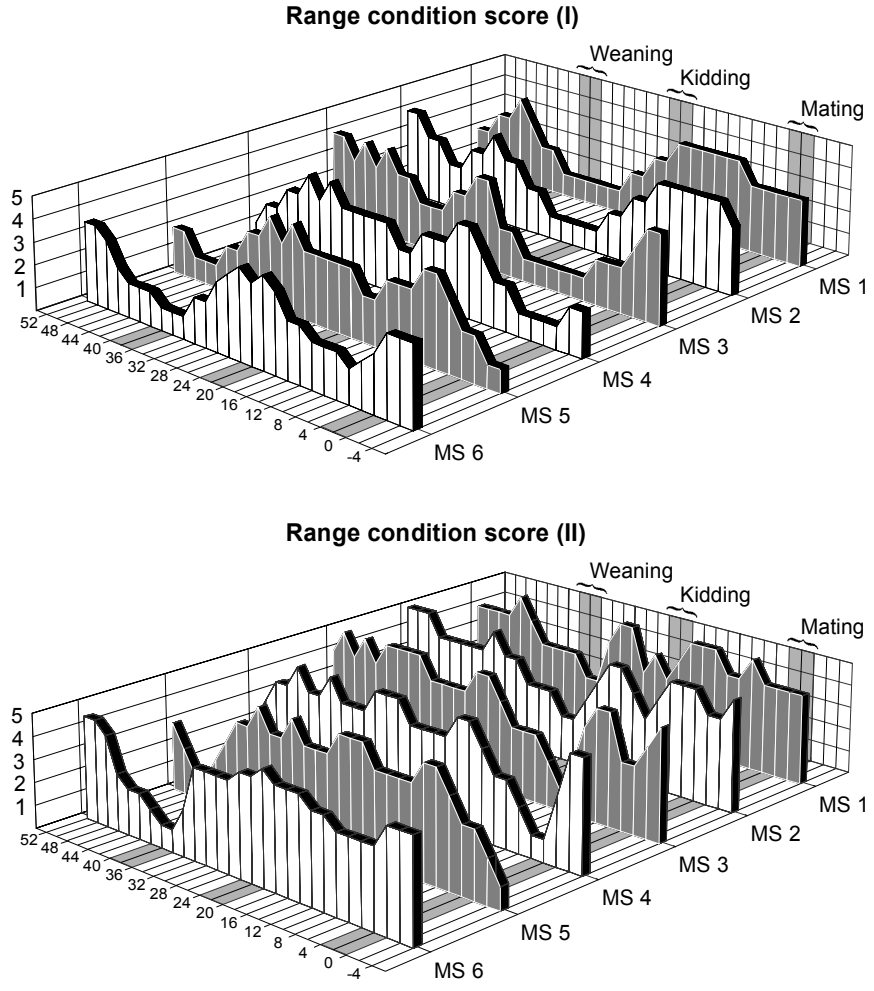

Figure 2.1. Observed median range condition in the herblayer (score [I]) and browse-adjusted range condition (score [II]) by mating season group (MS) over a production cycle of one year duration. Mating starts in week 0; the x-axis label "-4" refers to the time point four weeks prior to mating.

All other treatment groups gave birth under favourable environmental conditions typical of the short rains (group 3), the short dry season (group 4), as well as the beginning of during the long rainy season (groups 5 and 6). Kids born in mating season groups 2, 4, and 5 were weaned during periods with fair to good quality and quantity of forage on offer, such as prevails during the two rainy seasons. Increased availability of the high quality litter mentioned above helped to maintain range condition score [II] at fairly high levels toward the end of the long rainy season, when kids in group 5 were weaned. Somewhat less favourable pasture conditions were observed at the same production stage in group 3. In contrast, very poor forage conditions were encountered by kids born in groups 1 and 6, which were weaned in the middle and at the end of the long dry season, respectively.

Conception rate

The average ages at breeding, for animals in the various parity classes, for which age records were available were 67.8 weeks (SD 12.6) for first breeders, 117.6 (SD 19.3), 170.8 (SD 20.6), and 202.7 (SD 19.7) weeks for parity one to three animals, respectively. Only one age record was available for does with four or more prior kiddings (243 weeks). Mean body weights at breeding by parity stage are shown in Figure 2.2. Body weight was highest in third parity does with an average of about 38 kg and tended to decline thereafter. Of the 287 does mated during the experiment, 255 or 88.5 percent conceived. Except for range condition score [I], none of the fixed effects tested (parity; weight at breeding; lagged RC score [II]) had a significant influence on conception rate.

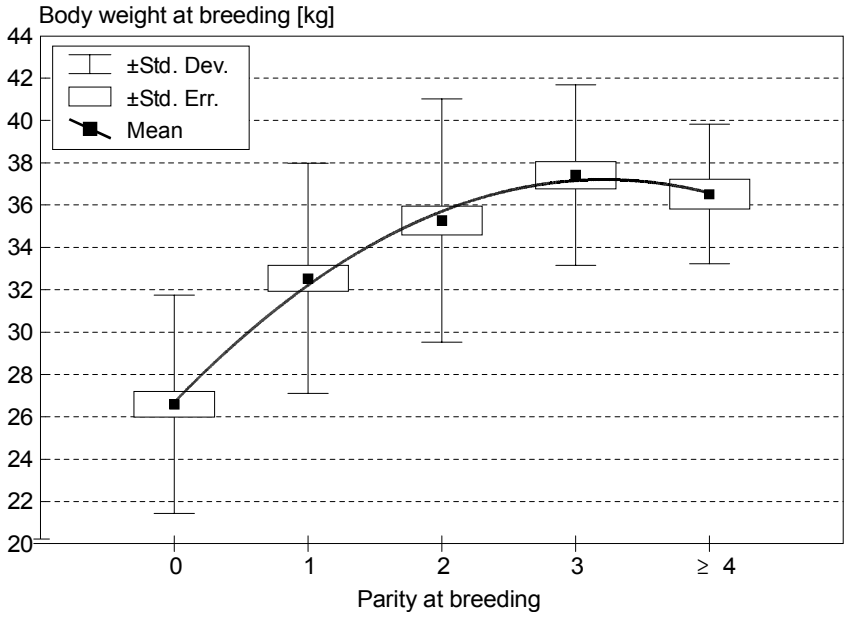

Figure 2.2. Box and Whisker plot of doe body weight at mating against parity number. The fitted function is a second-order polynomial.

Table 2.3. Analyses of deviance for logit models fitted to conception rates.

Model	df	Residual deviance	Source	Scaled χ^2	df	$p > \chi^2$
a)						
Intercept	286	200.69				
+ mating season	281	193.59	mating season	6.96	5	0.224
b)						
Intercept	286	200.69				
+ RC score [I]	283	190.24	RC score [I]	10.31	3	0.016

The mating season treatment and production cycle effects were also non-significant. The effect of lagged RC score [I] at mating on conception rates was analysed in a separate model (Table 2.3). As expected from the analysis of deviance for model *a)* in Table 2.1, none of the pairwise comparisons of expected conception rates across mating seasons were significant. However, the highest conception rate was observed when does were joined just before the onset of the long rainy season (mating season 1, Table 2.4), and the lowest when does were mated during the rainy and at the beginning of the dry season (mating season groups 2 and 3). Relatively high conception rates were observed in mating seasons four (0.89) and five (0.93), both of which were characterized by improving nutritional conditions around the time of mating, especially during the month of October.

Estimated conception rates in relation to lagged RC score [I] in Table 2.4 reveal a curvilinear trend, with the lowest values being observed under very poor and good range conditions, and the highest at intermediate scores of 2 and 3 (0.97 and 0.93, respectively). The latter were typically measured just prior and immediately after the rains, and thus typify situations in which forage conditions were gradually changing in direction of either the lower or upper extremes of the score scale.

Table 2.4. Parameter estimates for logit models fitted to conception rates (ϕ denotes the extra dispersion parameter).

Term		Estimate	Standard error	Estimated conception rate*)
a)				
Fixed effects:				
Mating season				
	1	3.239	0.797	0.962
	2	1.564	0.405	0.827
	3	1.792	0.452	0.857
	4	2.079	0.479	0.889
	5	2.590	0.662	0.930
	6	1.825	0.533	0.861
Dispersion components:				
ϕ		1.035	.	
b)				
Fixed effects:				
RC score [I]				
	1	1.846	0.378	0.864
	2	3.466	0.757	0.970^{a}
	3	2.398	0.450	0.917
	4	1.511	0.301	0.819^{b}
Dispersion components:				
ϕ		1.014		

*) Estimates without common letters in their superscripts differed at the five percent level of significance.

Abortion rate

A total of 15 abortion events out of 255 pregnancies (5.9 percent) were observed during the three production cycles. The small number of events made it difficult to fit higher level models to the data, and none of the effects tested, i.e. mating season, parity, doe body weight at mating, and lagged RC scores [I] and [II] at mating significantly affected abortion rates. The corresponding analysis of deviance is displayed in Table 2.5. The deviance of the mating season effect (MS) was substantially reduced after the non-constancy of mating season effects between production cycles (PC) was accounted for ($\sigma^2_{PC\times MS}>0$ versus $\sigma^2_{PC\times MS}=0$). Note that the production cycle dispersion component, σ^2_{PC}, was set to zero by the REML estimation procedure and therefore omitted from the final model. The PC×MS interaction was caused mainly by large differences in abortion rates among production cycles in mating season groups 4 and 5. As expected from the analysis of deviance, no significant difference in abortion rates between the six mating seasons groups was found (Table 2.6).

Table 2.5. Analyses of deviance for logit models fitted to abortion rates.

Model*)	df	Residual deviance	Source	Scaled χ^2	df	$p>\chi^2$
a)						
Intercept	254	114.10				
+ mating season	249	105.61	mating season	8.25	5	0.141
b)						
Intercept+$\sigma^2_{PC\times MS}$	254	99.65				
+ mating season	249	99.36	mating season	6.27	5	0.344

*) MS=mating season; PC=production cycle.

However, approximately 40 percent of all observed abortion events occurred in mating season 5, compared to 27 percent in mating season 4. Expected abortion rates in the latter two groups of approximately 15 and 9 percent, respectively, represented major productive inefficiencies. A comparison of model predictions pooled over mating seasons 4 and 5 on the one hand with those pooled over all other mating seasons on the other, revealed a significant difference at the 5 percent level ($F(1, 13.8)= 5.3$). In general, fetal losses increased as pasture condition scores declined around the time of mating (group 5) and during mid (group 4) and late pregnancy stages (group 3). The lowest abortion rates (< 3.5percent) were observed among goats mated during the short (group 6) or at the beginning and during the long rainy season (groups 1 and 2). In these cases, favourable forage conditions prevailed throughout the gestation period.

Table 2.6. Parameter estimates for the final model fitted to abortion rates.

Term		Estimate	Standard error	Estimated abortion rate
Fixed effects:				
Mating season				
	1	-3.911	1.053	0.020
	2	-3.741	1.057	0.023
	3	-2.994	0.781	0.048
	4	-2.348	0.590	0.087
	5	-1.736	0.529	0.150
	6	-3.390	1.074	0.033
*Dispersion components**)*:*				
ϕ		1.007		
$\sigma^2_{PC\times MS}$		0.246	0.642	

*) MS=mating season; PC=production cycle.

Birth rate

Overall birth rate in the experiment was 80.1 percent. Of the 255 breeding does that conceived, 21 aborted or died during pregnancy. Except for lagged range condition [I] at mating, the statistical analyses revealed no significant effect on birth rate of any of the explanatory variables considered. As before, the mating season treatment effect was retained in one of the two final models fitted to fertility data in order to provide smoothed estimates of birth rate for each mating season. Likewise to the analysis of conception and abortion rates presented above, the inclusion of the PC×MS interaction as a random effect led to a noticeable decrease in deviance for the mating season effect (Table 2.7). Although significant differences in expected birth rates between mating seasons were found when the fixed-effects model was fitted to the data, all pairwise comparisons were nonsignificant in the mixed-effects model.

Table 2.7. Analyses of deviance for logit models fitted to birth rates.

Model	df	Residual deviance	Source	Scaled χ^2	df	$p>\chi^2$
a)						
Intercept	286	274.60				
+matingseason	281	264.99	mating season	9.41	5	0.094
Intercept+$\sigma^2_{PC\times MS}$	286	233.03				
+matingseason	281	230.35	mating season	2.97	5	0.706
b)						
Intercept	286	274.60				
+ RC score [I]	283	259.26	RC score [I]	15.12	3	0.002

Table 2.8. Parameter estimates for final logit models fitted to birth rates.

Term	Estimate	Standard error	Estimated birth rate*)
a)			
Fixed effects:			
Mating season			
1	2.793	0.799	0.942
2	1.096	0.639	0.750
3	1.415	0.659	0.805
4	1.482	0.654	0.815
5	1.222	0.662	0.772
6	1.421	0.797	0.806
Dispersion components:			
ϕ	0.937		
$\sigma^2_{PC\times MS}$	0.937	0.576	
b)			
Fixed effects:			
RC score [I]			
1	0.906	0.272	0.712^a
2	2.303	0.428	0.909^b
3	2.228	0.398	0.903^b
4	1.083	0.253	0.747^a
Dispersion components:			
ϕ	1.007		

*) Estimates without common letters in their superscripts differed at the five percent level of significance.

Lagged range condition score [I] at mating was analysed separately, and was found to have a significant influence on birth rates ($p< 0.01$). Given that birth rate is a function of conception rate, abortion rate, and doe survival until parturition, some of the patterns described previously were carried over to the analysis of birth rates (Table 2.8). The high conception and fetal survival rates observed for mating season group 1, for instance, resulted in a high birth rate of approximately 95%. In contrast, the low number of fertilisations in group 2, as well as the high fetal mortality in mating season 5 were responsible for the comparatively poor performance of does joined during these periods. Large differences occurred between replications for does bred in mating season 5, with a very low birth rate of 43 percent in the second production cycle. Intermediate

levels of performance with birth rates averaging about 81 percent were observed in mating season groups 3, 4 and 6.

Lagged range condition score [I] at mating had an effect on birth rates similar to that it had on conception rates. Low and high values of this index corresponded to significantly lower birth rates than the intermediate values of 2 and 3. The latter, for instance, typically occurred around the time of mating in group 1, whereas scores of 1 and 4 characterised pasture conditions in groups 2 and 5, which achieved the lowest birth rates among all groups.

Prolificacy

The most frequent litter size was unity accounting for 59 percent of births, followed by 40.6 percent for twins and only one triplet, yielding an overall mean litter size of 1.44. Models fitted to prolificacy rates revealed a significant main effect of doe parity ($p< 0.01$), and main effects for lagged range condition scores [I] and [II] effects at mating (Table 2.9). Two separate models were fitted to the two range condition scores because of the high correlation between the two indices. After adjusting for the effect of range condition, additional dispersion components were set to zero by the REML estimation procedure (PC and PC×MS) and were, therefore, omitted from further consideration.

A third poisson regression model fitted contained mating season and doe parity at mating as the linear predictors. Mating season neither significantly affected predicted prolificacy rates in the fixed effects models, nor in the model incorporating the random PC×MS interaction. In contrast, differences between parity numbers remained highly significant in both of these models.

Body weight at mating exerted a significant effect ($p< 0.01$) when no allowance was made for the effect of parity on prolificacy rates, but was nonsignificant ($p> 0.5$) after adjusting for the latter. This result was largely due to the strong positive correlation between body weight at mating and parity (see Figure 2.2). Conversely, the effect of parity on prolificacy was not influenced by the weight at mating term. Based on this finding, it

Table 2.9. Analyses of deviance for Poisson regression models fitted to prolificacy rates.

Model	df	Residual deviance	Source	Scaled χ^2	df	p>χ^2
a)						
Intercept	67	17.05				
+matingseason+parity	58	9.28	mating season	7.42	5	0.191
			parity	38.38	4	<0.001
Intercept+σ^2PC×MS	67	16.50				
+matingseason+parity	58	7.73	mating season	4.73	5	0.450
			parity	42.69	4	<0.001
b)						
Intercept	67	17.05				
+RCscore[I]+parity	60	8.97	RC score [I]	10.00	3	0.019
			parity	46.94	4	<0.001
c)						
Intercept	67	17.05				
+RCscore[II]+parity	59	9.34	RC score [II]	6.86	4	0.143
			parity	45.15	4	<0.001

was concluded that the effect of weight at mating was confounded with that of parity. Therefore, only the latter term was retained in the final models presented in Table 2.9. Does bred in the first mating period, just prior to the long rains, produced the largest litter size per birth event (1.58 kids, Table 2.10). The conspicuous depressing effect of mating season 2 (1.30 kids) on prolificacy was unexpected, since, in this group, does were joined at the peak of the long rainy season when, in general, good feeding conditions prevailed. The fact that fairly large numbers of twin birth events occurred in mating groups 4 and 5 was also unexpected given that these seasons coincided with the middle and the end of the long dry season, respectively. Prolificacy

rates in mating seasons 3 to 6 showed only minor deviations from the predicted mean value over these four groups of 1.45. With respect to lagged range condition scores at mating, the patterns described previously for other traits persisted in the analysis of prolificacy rates.

Table 2.10. Parameter estimates for final models fitted to prolificacy rates.

Term	Estimate	Std. error	Estimated prolificacy rate*)	Term	Estimate	Std. error	Estimated prolificacy rate*)
a)							
Fixed effects:							
Mating season				parity			
1	0.460	0.062	1.58	0	0.128	0.051	1.14^{a}
2	0.266	0.068	1.30	1	0.266	0.047	1.30^{a}
3	0.379	0.066	1.46	2	0.430	0.046	1.54^{b}
4	0.387	0.062	1.47	3	0.531	0.054	1.70^{b}
5	0.352	0.071	1.42	≥4	0.482	0.076	1.62^{b}
6	0.362	0.080	1.44				
Dispersion components:							
ϕ	0.145						
σ^2PC×MS	0.0047	0.0056					
b)							
Fixed effects:							
RC score [I]				parity			
1	0.335	0.050	1.40	0	0.127	0.047	1.14^{a}
2	0.408	0.041	1.50	1	0.263	0.044	1.30^{a}
3	0.469	0.044	1.60^{a}	2	0.437	0.042	1.55^{b}
4	0.292	0.044	1.34^{b}	3	0.544	0.051	1.72^{b}
				≥4	0.508	0.072	1.66^{b}
Dispersion components:							
ϕ	0.150						
c)							
Fixed effects:							
RC score [II]				parity			
1	0.323	0.091	1.38	0	0.104	0.048	1.11^{a}
2	0.250	0.075	1.28	1	0.243	0.045	1.27^{a}
3	0.391	0.050	1.48	2	0.412	0.042	1.51^{b}
4	0.440	0.034	1.55	3	0.505	0.051	1.66^{b}
5	0.342	0.037	1.41	≥4	0.481	0.071	1.62^{b}
Dispersion components:							
ϕ	0.157						

*) Estimates without common letters in their superscripts differed at the five percent level of significance.

Very poor (level 1) and favourable (level 4) pasture conditions prior to mating had a depressing effect on prolificacy. A significant difference was found between the largest litter sizes predicted for level 3, and the lowest ones predicted for level 4. The relation between RC score [II] and conception rates was less consistent (p>0.1) and, consequently, no significant differences among score levels could be detected. However, estimated mean litter sizes across RC score [II] levels displayed an overall pattern similar to that observed for RC score [I].

The most important influence on prolificacy rates was exerted by parity number. As can be seen from Table 2.10, predicted values of prolificacy rates by parity number remained relatively consistent across all three

models, indicating a very small dependence of model predictions for this term upon other explanatory factors. A considerable increase occurred in prolificacy rates with increasing number of lactations, starting from a minimum of 1.1 kids per birth for first breeders to a maximum of about 1.7 kids per birth at the fourth kidding. Litter sizes declined in older does with at least four prior kiddings. Orthogonal polynomial contrasts revealed significant linear ($F(1, 52.2)=26.5$) and quadratic ($F(1, 54.5)=4.3$) trends in prolificacy rates with increasing parity stage.

In order to ascertain that no differential effects of body weight at mating were present within each of the five parity classes, all observed combinations of body weight and parity levels were combined into a single variable with 20 levels. A model including the mating season effect and the weight-within-parity variable was then fitted to the prolificacy data. The weight-within-parity variable was found to be highly significant ($\chi^2=61.8$, df=19). However, no significant differences in mean prolificacy between body weights within parity levels could be detected.

Fecundity

Fecundity rate is a function of birth rate and prolificacy. The results of the statistical analysis presented below thus summarize, in a way, the joint effects of these two traits. As might be expected from the foregoing, the analysis revealed no significant effect of mating season once adjustment was made for the random PC×MS interaction (Table 2.11). In contrast, the significance of parity number was not affected by the inclusion of this dispersion component. The production cycle dispersion component, σ^2_{PC}, was set to zero by the REML estimation procedure and therefore omitted from the final model.

Since body weight at mating and parity were confounded, the former effect was not considered in the analysis. Furthermore, no significant effect of range condition score [II] was found. The analysis of deviance (Table 2.11) for the model containing RC score [I] and parity number revealed significant effects of both variables on predicted fecundity rates ($p< 0.05$). Parameter estimates in Table 2.12 show that the predicted response patterns of fecundity rates across mating season groups resembles that described previously for birth and prolificacy rates.

Does bred in the first mating period performed particularly well, with an expected number of kids born per doe exposed of 1.46. In contrast, reproductive efficiency was severely reduced when does were mated at the peak of the long rainy season (group 2). Although not statistically significant, the difference between these

Table 2.11. Analysis of deviance for models fitted to fecundity rates.

Model	df	Residual deviance	Source	Scaled χ^2	df	$p>\chi^2$
a)						
Intercept	67	52.89				
+matingseason+parity	58	40.71	mating season	9.90	5	0.078
			parity	11.30	4	0.023
Intercept+σ^2PC×MS	67	32.51				
+matingseason+parity	58	26.40	mating season	3.58	5	0.626
			parity	11.87	4	0.028
b)						
Intercept	67	52.89				
+RCscore[I]+parity	60	37.63	RC score [I]	16.53	3	0.001
			parity	12.48	4	0.014

Table 2.12. Parameter estimates for final models fitted to fecundity rates.

Term		Estimate	Std. error	Estimated fecundity rate*)	Term	Estimate	Std. error	Estimated fecundity rate*)
a)								
Fixed effects:								
Mating season					parity			
	1	0.381	0.155	1.46	0	-0.031	0.101	0.97^{a}
	2	-0.027	0.163	0.97	1	0.023	0.095	1.02^{a}
	3	0.171	0.161	1.19	2	0.231	0.092	1.26
	4	0.204	0.155	1.23	3	0.323	0.106	1.38^{b}
	5	0.069	0.168	1.07	≥4	0.251	0.145	1.29
	6	0.159	0.196	1.17				
Dispersion components:								
ϕ		0.442						
σ^2PC×MS		0.056	0.033					
b)								
Fixed effects:								
RC score [I]					parity			
	1	-0.002	0.093	1.00^{a}	0	-0.033	0.088	0.97^{a}
	2	0.314	0.076	1.37^{b}	1	0.001	0.081	1.00^{a}
	3	0.371	0.081	1.45^{b}	2	0.219	0.078	1.24
	4	0.008	0.080	1.01^{ac}	3	0.370	0.094	1.45^{b}
					≥4	0.305	0.134	1.36
Dispersion components:								
ϕ		0.586						

*) Estimates without common letters in their superscripts differed at the five percent level of significance.

two treatment groups was substantial, amounting to 0.49 kids per doe exposed. Comparatively high fecundity rates were also achieved in group 4. Estimates for groups 3, 5, and 5 were of similar magnitude but somewhat lower than those for groups 1 and 4. Predictions for the former were quite unreliable, as can be seen from the standard errors of the predicted means. Parity number had an outstanding effect on fecundity rates, which, based on estimates accounting for the effect of mating season, ranged from 0.97 kids per doe exposed for first parturitents, to 1.38 kids per doe exposed for breeding females with three prior kiddings. A significant overall linear trend across parity levels was demonstrated ($F(1, 54.5)=6.51$), but not the presence of a quadratic curvature, suggested by the observed decline in theresponse of does with at least four prior kiddings, had to be rejected. Mean separation tests showed significant differences in the expected numbers of kids born per doe exposed belonging to levels 1 and 4 versus levels 2 and 3, respectively, of range condition score [I] at mating. The highest fecundity rates were achieved for a score of 3 at mating.

Weaning rate

The number of offspring weaned per doe exposed is a measure that combines two components of reproductive performance, fecundity and postnatal survival of kids. Survival rates of kids until weaning are discussed in Chapter 3, and a detailed account of the factors affecting kid survival, and thus weaning rate, is therefore deferred to that chapter.

In the fixed effects model, only parity exerted a significant effect on weaning rates (Table 2.13). For the same reasons as before, weight at breeding was dropped from the final model. The variation due to production cycle and its interaction with mating season caused the parity main effect to become insignificant and, consequently, pairwise comparisons of expected weaning rates across parity numbers failed to reveal any significant differences (Table 2.14). However, does with higher lactation numbers seemed to achieve better weaning rates than those in the first and second lactation. The response peaked for fourth parity, and declined

afterwards. The slightly lower expected response for primiparous does compared to first breeders was suspected to be related to an interaction between mating season and parity number. Although the interaction term appeared to be an unimportant source of variation (p=0.303), a test of simple effects showed a substantial difference in weaning rates between the first two parity levels within mating season four (parity0=0.928; parity1=0.436). This might account for the observed attenuation of the response for primiparous females.

Table 2.13. Analysis of deviance for Poisson regression models fitted to weaning rates.

Model	df	Residual deviance	Source	LR	df	$p>\chi^2$
Intercept	70	60.42				
+matingseason+parity	61	47.01	matingseason	9.12	5	0.105
			parity	9.87	4	0.043
Intercept+σ^2_{PC}+$\sigma^2_{PC\times MS}$	70	34.93				
+matingseason+parity	61	32.59	matingseason	5.77	5	0.404
		parity	5.41	4	0.263	

When compared to fecundity rates in Table 2.12, a considerable change in relative performance of does bred in the six mating seasons is apparent. High mortality rates in kids obviously depressed the reproductive efficiency of animals joined in the first and sixth period, with expected weaning rates of 0.77 and 0.82 kids weaned per doe exposed, respectively. Weaning rates in mating season groups 2 and 3 were also affected by elevated kid mortality, although to a lesser extent. The best performance was achieved by does mated in the middle of the long dry season in mating season group 4, with a predicted weaning rate of 1.12 kids weaned per doe exposed.

Table 2.14. Parameter estimates for final Poisson regression models fitted to weaning rates.

Term		Estimate	Standard error	Estimated weaning rate
Fixed effects:				
Mating season				
	1	-0.256	0.200	0.77
	2	-0.278	0.199	0.76
	3	0.008	0.195	1.01
	4	0.109	0.186	1.11
	5	-0.035	0.199	0.97
	6	-0.198	0.230	0.82
Parity				
	0	-0.164	0.168	0.85
	1	-0.289	0.166	0.75
	2	-0.069	0.163	0.93
	3	0.034	0.176	1.03
	4	-0.053	0.219	0.95
Dispersion components:				
ϕ		0.526		
σ^2_{PC}		0.062	0.074	
$\sigma^2_{PC\times MS}$		0.025	0.030	

2.4 Discussion

Measurement of reproductive performance

A high rate of reproductive efficiency is often thought to be the most important prerequisite for the production of meat. milk, skins, and breeding stock (Terrill & Foote, 1987; Steinbach, 1988; Wilson, 1989). The term reproductive efficiency, however, is often poorly defined in the literature (Baptist, 1992*b*), and a confusing multitude of different measures have been employed in livestock production studies, some of which have recently been reviewed by Bosman et al. (1997). Steinbach (1988) for instance, in assessing reproductive performance equates the term "biological productivity" with weaned weight per metabolic doe weight per year. Similar indices have also been used by Knipsheer et al. (1984), Peacock (1987), and Wilson (1984). Strictly speaking, these types of indices do not qualify as true measures of technical (biological) efficiency of reproduction in livestock herds, since they do not relate outputs yielded to inputs required in the production process (Baptist, 1992*b*). More precisely, they reflect yield levels but fail to relate this to a given level of production inputs. Measuring reproductive performance in terms of a compound measure such as weaned weight per breeding female (or unit metabolic weight thereof) provides little insight into the relative importance and impact of component traits on the calculated value (Bosman et al., 1997b) and, additionally, implies a value judgement as to the objectives of the decision maker. For instance, while maximisation of output in terms of weaned liveweight can be a relevant criterion in commercial meat production systems, this is not necessarily true in dairy or dual-purpose operations, and even less so in subsistence oriented production systems (Behnke, 1985).

In the present study the effect of seasonal breeding on reproduction was evaluated in relation to specific responses that are linked to physiological processes affecting reproductive performance, such as ovulation rate, fertilization rate, embryonic and/or fetal survival, and proportion of dams and offspring surviving to parturition. Defining reproductive performance in its most specific components bears several advantages in this context. Firstly, the level of resolution provided by this approach facilitates the identification of factors influencing the biological potential of a herd to produce offspring, and allows the assessing of how these factors are affected by experimental treatments. Also, for analytical purposes, it would seem appropriate to isolate reproductive responses from kid survival and growth, because the component of environmental variance attached to the latter two traits is often high. Secondly, whereas the estimation of parameters such as probability of conception and abortion, birth rate, prolificacy, and fecundity is straightforward, special problems arise in defining measures such as kidding rate (offspring born per breeding female per time unit) and kidding interval (average time interval between parturitions) which, in many cases, are required for computing compound indices of reproductive performance. For instance, Baptist (1988) and Upton (1989) demonstrated that failure of taking into account fractions of temporarily unreproductive as well as sterile females in a herd are sources of inconsistencies and errors in estimating kidding rate and kidding interval.

General impact of environmental conditions on reproduction

Reproductive performance in goats is a composite of several processes which are influenced by environmental, developmental, genetic, and managerial factors (Terril & Foote, 1987). The present work focused on investigating the influence of management (mating season), environment (range condition) and developmental history (parity) on these traits. The mating season treatment was hypothesized to act on reproductive performance by altering the nutritional status of dams around breeding and throughout the pregnancy stage, while range condition was assumed to be an indicator of nutritional conditions prevailing just prior to mating only. However, mating season did not exert a significant influence on any of the traits analysed. Except for conception rates, all models fitted revealed a substantial variation in the mating season effect across production cycles, thus suggesting that inter-year variability in environmental conditions was very large and hence masked a clear expression of differential effects on reproductive function of controlled breeding. In contrast, range condition, and thus forage quantity and quality on offer, during the pre-mating period significantly affected some of the reproductive responses analysed (conception rate, birth rate, prolificacy, and fecundity). This is not surprising, since it is a well established fact that in the absence of photoperiodic cuing, nutrient supply is the main environmental regulator of all aspects of reproduction (Walkden-Brown & Restall, 1996). According to Bronson (1989), a reproductive strategy that is not regulated by seasonal predictors, photoperiod or otherwise, can be classified as opportunistic. In its extreme form, opportunism dictates that males remain sexually ready at all times of the year, and that the breeding behaviour of females is responsive to short-term changes in energetic and nutritional conditions.

Conception rate

The conception rates in excess of 82 percent across all mating season groups are a clear evidence of non-seasonality of reproduction in SEA goats. Moreover, since conception rate was defined as the fraction of does kidding and aborting relative to the total number of does present at mating, without taking into account embryonic and fetal losses that may have occurred, it is likely that the conception rates predicted for each mating season group underestimated the true rates of fertilization achieved during the experiment. Unfortunately, there are only few reports available to which the present results could be compared. This is partly due to the fact that most of the relevant reports do not provide figures on conception rates achieved in the flocks under study, but only birth or kidding rates, or merely production indices (e.g., Mellado et al., 1991, 1996; Ndlovu & Simela, 1996; Sachdeva et al., 1973; Wilson, 1989; Wilson et al., 1984; Wilson & Light, 1986). On the other hand, experimental studies dealing with aspects of reproductive physiology in tropical, non-photoresponsive goat breeds are scarce (Walkden-Brown & Restall, 1996; Wilson, 1989).

Nevertheless, Peacock (1984) investigated the reproductive performance of Maasai SEA goat flocks which were exposed to a buck during the months of July and August. Her results can thus be compared to those obtained for mating season group 4 in the present study. The author analysed the reproductive performance achieved in two different groups of flocks. One had been moved to pastures on which *Acacia tortilis* was one of the dominant plant species in order to allow the goats to feed on the high quality litter, predominantly *Acacia tortilis* pods shed by these trees at the peak of the long dry season. The other group was herded on pastures on which animals had no access to *Acacia tortilis* litter. The analyses revealed that in two flocks of pod-fed animals about 77 and 83 percent of the does conceived, compared to only 20 percent in the flocks not pod-fed. As the major difference between the two treatments was in the animals actually mated, Peacock (1984) concludes that the consumption of pods mainly affected the occurrence of oestrus. By comparison, the conception rates achieved in the pod-fed flocks are somewhat lower than those predicted for mating season group 4 in the present study (89 percent). The comparatively good performance of this group was surprising, since one would have expected that the poor nutritional conditions prevailing at the peak of the long dry season, and their associated effect on body condition of does, should have had a deleterious impact upon oestrus activity, ovulation, and fertilization rate, such as was reported, for example, by Sachdeva et al. (1973)

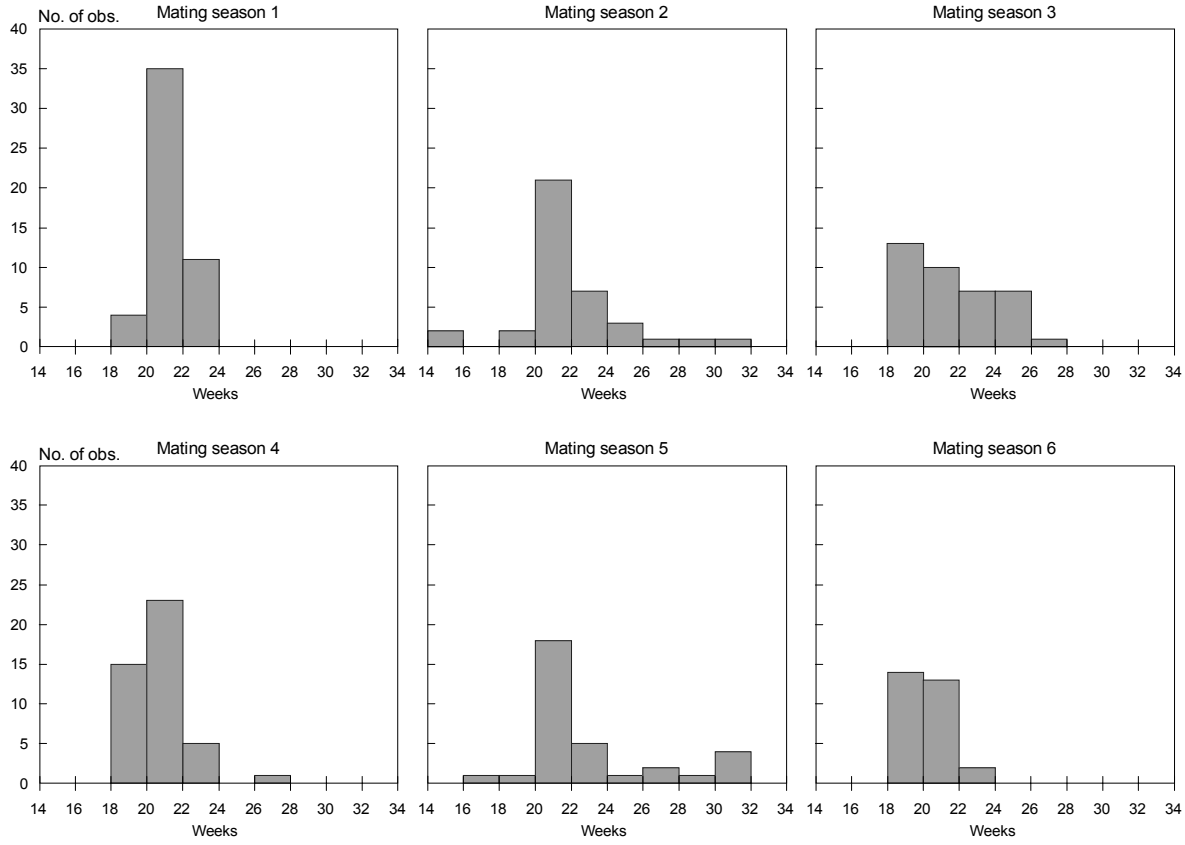

Figure 2.3. Frequency distribution by mating season of the duration between onset of mating and parturition in fertile females.

and Mani et al. (1992). Peacock's study provides at least a partial explanation for this phenomenon, in spite of the fact that the browse adjusted range condition score [II], which was supposed to reflect changes in the availability of high quality litter, did not exert a significant influence on conception rates.

Although differences in conception rate among treatments were not statistically significant, it is notable that conception was minimal when does were joined under the most favourable forage conditions. Only 83 percent of the does mated at the peak of the long rainy season in April (mating season 2) became pregnant, and a similar value (82 percent) was predicted for a median pre-mating range condition score [I] of 4. Conversely, maximum conception rates occurred in groups mated during the short (group 1) and towards the end of the long dry season (group 5), or for median pre-mating range condition scores [I] of 2 or 3. In mating season group 5, however, nutritional anoestrus may initially have occurred in some of the does exposed as suggested by the distribution of the duration between first exposure to the buck and parturition, depicted in Figure 2.3. Given that the length of the breeding period was two months, and assuming a gestation period of roughly 22 weeks, does giving birth after more than 28 weeks must have been mated towards the end of the breeding period, which, in case of group 5, coincided with the peak of the short rainy season in November. Resumption of ovarian and oestrus activity thus may have occurred in response to improving nutritional conditions. It is also interesting to note that in most fertile females joined during the short (group 1), at the middle of the long dry season (group 4), as well as towards the end of the short rainy season (group 6), fertilization must have occurred within a few weeks from the onset of mating. In contrast, the proportion of non-cycling does appears to have been larger throughout the long rainy season (groups 2 and 3).

These results suggest, firstly, that whenever feeding conditions start to improve oestrus and ovulation are positively affected. The sexual activity of SEA goats thus seems to be sensitive to short-term changes in nutrient supply. This observation fits well into the theoretical framework advanced by Bronson (1989), which postulates that in the absence of photoperiod as a predictive cue, external climatic and dietary factors may act as predictors of conditions promoting reproductive success in mammals. Such an opportunistic reproductive strategy may also rely on short-term predictors obtained from plants. Based on Bronson (1989), the use of plant predictors can be expected to be particularly advantageous for strict herbivores of short life span that live in highly unpredictable environments. Also, previous studies on goats reviewed by Walkden-Brown and Restall (1996) provide some evidence that the sudden availability of good nutrition may induce oestrus and ovulation in non-photoresponsive breeds. According to Landau et al. (1996), these short-term effects are achieved through provision of nutrients that modify the hormonal environment, with no alteration of body condition. In a similar vein, Peacock (1984) conjectured that the improved reproductive performance of goats fed on *Acacia tortilis* pods prior to mating could have been due to the high protein content of the pods and/or to their content in compounds with possible oestrogenic properties. It is worth noting that nutritional supplementation may also improve oestrus activity and ovulation rate in females indirectly through the so-called male effect. Walkden-Brown et al. (1993) reported higher oestrus responses and conception rates in Australian Cashmere goats exposed to bucks fed a high quality diet compared to bucks fed a low quality diet.

Secondly, abundant availability of good quality forage over prolonged periods (>4 weeks) before mating seems to have a detrimental effect on oestrus activity and ovulation. This longer term nutritional effect on reproductive function is likely to be mediated through improved body condition (Landau et al., 1996; Walkden-Brown et al., 1996). The contention that high levels of body condition may be responsible for reduced oestrus activity and fertilization rate in goats is difficult to corroborate from the literature. Landau et al. (1996) state that no negative effect of over-condition on reproductive performance appears to have been documented for goats, as has been done for sheep. Rhind et al. (1984), for example, found that excessively high levels of body condition of ewes at mating can have detrimental effects on both oestrus activity and ova or embryo survival. Adverse effects of high body condition on conception rates in sheep have also been reported by Gunn et al. (1991). In contrast, Henniawati and Fletcher (1986) showed that a supramaintenance level of feeding throughout the pre-mating and mating period had no effect on the incidence of oestrus in Indonesian sheep and goats, but significantly increased mean ovulation rate in both species, a fact reflected in subsequent lamb and kid production. In view of these inconsistent results it is difficult to rationalise the observed reduction in conception rates in does exposed to favourable forage conditions over a prolonged period prior to mating. More research is needed to strictly characterise the relationship between seasonal forage supply, body condition and conception rates in goats maintained on semi-arid tropical pastures.

Prolificacy

Generally, the appearance and continuation of oestrus activity in goats has been reported to be less dependent on nutrition than does ovulation rate (Landau et al., 1996). Although the physiological mechanisms by which nutrition affects ovulation rate are not yet fully understood (Dunn & Moss, 1992; Mani et al., 1992), improved nutrition has been found to increase ovulation rate and the incidence of multiple births in goats. Besides the study of Henniawati and Fletcher (1986) noted above, Sachdeva et al. (1973) also hold the view

that a high plane of nutrition, particularly with respect to the energy content of the diet, increases the number of twin birth events. In the present study, the models fitted to prolificacy rates confirmed these findings in that litter size increased with increasing pasture quantity and quality during the pre-mating period, as expressed by the parameter estimates for levels 1 through 3 (score I) and levels 1 through 4 (score II) of the two range condition scores. However, the decline in litter size associated with levels 4 and 5 of range condition scores I and II, respectively, that were presumed to reflect maximum availability of forage of good quality, are inconsistent with the reports noted above. This tendency was also expressed in the estimated prolificacy rate of mating season group 2 (1.3 kids per birth), as opposed to that achieved in all other groups (>1.4 kids per birth). Likewise to conception rates, corroborative evidence for a depressing effect of excessive body condition or high planes of nutrition on ovulation rate, and/or embryonic and fetal survival, and hence the probability of multiple birth events in goats seems to be unavailable at this time.

The fact that fairly large litter sizes were observed for mating season groups 4 and 5 was also surprising given that mating in these groups coincided with the middle and end of the long dry season, respectively. A possible explanation for this pattern is that the consumption of high quality litter from *Acacia* species could have had a stimulating effect on ovulation rates. Also, the superior quality of different plant parts of *Acacia* species that are consumed by goats during the long dry season tends to upgrade and balance the deteriorating quality of other forages in the diet during this time (Schultka & Schwartz, 1987), and may have prevented excessive losses in body condition before mating. However, the point to be made here is that no clear picture has emerged yet as to the mechanisms by which changes in plane of nutrition, body condition score, and body weight affect ovulation rate in livestock (Dunn & Moss, 1992). Although body condition was not assessed in this study, the responses for mating season group 4 in particular seem to suggest that short-term changes in feeding conditions could exert a more direct influence on ovulation rate than body condition status at mating. Supportive evidence for a rise in ovarian activity during the dry season was reported by Hambolu and Ojo (1985, p. 281), who attributed the observed pattern to the higher temperature and the "ability of goats to convert any available leaves and dry forage into useful nutrients during the dry season". On the other hand, Peacock (1984) did not observe higher twinning rates in goats fed on high quality *Acacia* litter prior to mating during July and August, which conflicts with the statement made above that there exists a short term nutritional effect on ovulation rate.

Apart from the above anomalies in responses, the present work confirmed the finding of Wilson et al. (1984) that litter sizes in SEA goats were greatest for parturitions taking place in both dry season (groups 1 and 4). With 1.44 kids per birth, however, average litter size was markedly larger than the 1.23 kids per birth recorded in the latter study. In contrast to other African breeds, such as Red Sokoto and West African Dwarf goats, which have been reported to produce 1.56 (Adu et al., 1979) and between 1.53 and 1.89 kids per birth (Bosman, 1995), respectively, triplet birth events seem to occur very rarely in SEA goats. Only one triplet litter out of 234 kiddings was observed in the present study. The overall probability of twin birth events of about 41 percent is comparable to the twinning rate of 30 percent estimated by Sacker and Trail (1966) for Mubende SEA goats in Uganda, whereas Ndlovu and Simela (1996) reported a twinning rate of only 3 percent for Mashona goats in Zimbabwe. Hence, the genetic potential for prolificacy of the SEA breed type appears to be inferior to that of other African breeds, particularly to that of many West African breeds. In any case, according to Bradford and Berger (1988) prolificacy in excess of twins is not desirable in goats dependent on grazing in arid lands, and the primary management goal should be the achievement of a mean prolificacy of 1.5-1.8 kids born per parturition. On average, the performance of SEA goats observed herein is close to the lower end of this range, while at third and later kiddings does can be expected to produce up to 1.7 kids per parturition.

The observed quadratic trend in litter size with increasing number of lactations is well established, and has been reported, among many others, by Wilson et al. (1984) for SEA goats, by Wilson (1984) and Wilson and Traoré (1988) for Sudan desert and Sahel goats, and by Adu et al. (1979) for Red Sokoto goats. Also, Osuagwuh (1991) found that the incidence of multiple births increased linearly with doe age. Given that the probability of a twin birth event increased from 14 percent at first to 69 percent at fourth kidding, doe parity appears to be one of the most important variables determining litter size in SEA goat herds. This emphasizes the importance of taking into account the relative abundance of does in different parity stages when making productivity assessments in goat herds. In comparative trials, performance criteria computed by averaging over the entire breeding female herd are likely to produce biased results and, therefore, invalid inferences, if relative parity stage abundances in the flocks considered are different, or, alternatively, if they are not in a stable state.

Other studies have reported an increase in litter size with liveweight of dams at mating, presumed to be indicative of body condition (e.g., Adu et al., 1979; Amoah et al., 1996). Similarly, changes in liveweight during the pre-mating period have been assumed to reflect changes in body condition. However, as has been pointed out by Devendra and Burns (1983), liveweight and age, and liveweight and parity number tend to be

confounded. Since the liveweight of breeding females is generally positively correlated with the number of parturitions or age, it is unclear to what extent an increase in multiple birth events can be attributed to physiological maturity, body weight or body condition at the time of mating. The statistical analysis performed in the present study did not reveal a significant effect of liveweight within parity class on prolificacy rates. Hence, liveweight at mating appears to be a poor predictor of litter size, after adjusting for the effect of parity. It is also doubtful whether this variable can be used as an indicator for body condition. Body weight is mainly determined by frame size, conformation, and relative fatness. It follows that a small body weight can be due to either a poor body condition or a small frame with adequate condition (Gunn & Moss, 1992). Moreover, the assumption that a change in body weight can be treated as an indicator for a concomitant change in body condition appears to be problematic, since, as has been demonstrated in the present study, body weight changes in does at all stages of the reproductive cycle are closely related to their parity stage (see Chapter 4). As such, it is suggested that parturition number is an important source of variation in reproductive responses in goats that should be controlled for experimentally.

Abortion and birth rate

Since embryonic and fetal mortality rates were not determined, the estimates obtained for birth rate were a function of (apparent) conception rate, abortion rate, and survival of pregnant does until parturition. The overall mean abortion rate of 5.9 percent was within the range reported in the literature on African goat breeds. Osuagwuh (1991) observed an incidence rate of 4 and 2.3 percent in 1.5 and 4 year old West African Dwarf goats, whereas that recorded by Traoré and Wilson (1988) in a Mali traditional system was much higher at 12.6 percent. Abortion rates were generally low (< 3.5 percent) when moderate to good feeding conditions prevailed at mating and throughout the gestation period (mating season groups 1, 2 and 6), while a noticeable increase in incidences occurred with further displacement of mating into the long dry season (mating season groups 3, 4 and 5). At 8.7 and 15 percent of all pregnancies, the number of incidences in mating season groups 4 and 5 was particularly high. The majority of the abortion events occurred during late pregnancy which, in these two groups, coincided with the onset of the short and long rainy season, respectively. Hence, it is unlikely that abortion was linked to poor nutrition and starvation. At the beginning of the rainy seasons in semi-arid climates, animals change from a dry and limited diet to a green and abundant one, which is usually rich in nitrogen but poor in fibre. According to Lebbie et al. (1996), such a rapid modification of the ration can lead to an outbreak of enterotoxemia, caused by a sudden increase in the *Clostridium perfrigens* population in the intestine where the fast growing bacteria produce toxins which diffuse into the blood. This disease as well as other metabolic disturbances linked to nutritional disorders may have precipitated the incidence of abortions in groups 4 and 5.

Estimated doe mortality during the gestation period was of the order of 4 to 5 percent (mating season groups 2 and 3, respectively) when mid- and late pregnancy stages occurred during the long dry season, and less than 2 percent otherwise. The effects of high abortion rates and/or high doe mortality until parturition on weaning rates were most pronounced when does were joined towards the end of the long dry season (mating season group 5), in which case on average only 83 percent of the observed pregnancies were carried to term, while animals mated just prior to the long rains were least affected, with a birth rate of 98 percent in fertile does. In the other four groups, about 90 (group 2), 94 (groups 3 and 6), and 92 percent (group 4) of the pregnancies were estimated as having been carried to term.

The estimated birth rate for mating season 4 (77 percent) is in agreement with observations made by Peacock (1984) on two flocks of SEA goats mated during the long dry season and fed on high quality *Acacia* litter prior to mating, which achieved birth rates of 75 and 83.3 percent. It is noteworthy that the birth rate in goats mated at the same time, but which had no access to *Acacia* litter was as low as 13.3 percent. In both treatments, prenatal reproductive wastage in fertile does was limited to the occurrence of abortions, which were recorded to be 2.1 and 0 percent in the flocks fed on *Acacia* litter, and 6.7 percent in the other group. Likewise to conception rates, other studies, including the review of Wilson (1989) on reproductive performance of African indigenous small ruminants, conducted previously on African goat breeds kept under similar environmental conditions do not provide information on birth rates (e.g., Wilson et al., 1984; Wilson & Light, 1986; Wilson & Traoré, 1988; Ndlovu & Simela, 1996). However, overall birth rate in SEA goats appears to be high and is comparable to the 83.8 percent achieved after artificial insemination with follow-up mating by 20 months old Cashmere goats in a temperate environment in Australia (Ritar et al., 1994). Under arid conditions in northeast Mexico, a similar performance (82 percent) was recorded by Mellado et al. (1994) in crossbred goats in good body condition at mating, whereas poor body condition at mating resulted in a birth rate of only 46 percent. As reported by Mellado et al. (1996), the length of the breeding period appears to be a decisive factor in determining reproductive performance in goats kept under extensive range conditions. Birth rate was severely depressed when the mating period was less than 21 days. Indeed, the distribution of the duration between the onset of mating and parturition in fertile females observed in the

present study (Figure 2.3) underlines the importance of extending the breeding period beyond the average length of one oestrus cycle under controlled breeding. For instance, allowing non-cycling does to return to service was certainly an important factor in maintaining satisfactory conception rates in does mated at the end of the long dry season (mating season group 5).

Fecundity

In spite of the fact that differences in fecundity rates between mating season groups failed to reach statistical significance, it is nevertheless clear that mating at the start of the long rainy season by far produced the largest number of kids per doe exposed (1.46, mating season group 1). Controlled breeding under semi-arid conditions in northern Kenya clearly has a detrimental effect on fecundity when goats are joined in the middle of the long rainy season. The results obtained in this study indicate that restricting breeding to this period can be expected to lead to fecundity rates of less than unity. Estimates obtained for does joined between the months of June to December (groups 3 to 6) exhibited only small differences, with the exception of the depressed performance caused by an elevated incidence of abortions during pregnancies that were established at the end of the long dry season in October (group 5). Also, the patterns reflected by fecundity estimates across lagged median range condition scores at the time of mating have to be interpreted in relation to the change in range condition scores throughout the gestation period. Favourable forage conditions at mating, as observed in group 2, produced the lowest fecundity rates. Contrary to what might be expected, this apparently was due only in part to the fact that in this case late pregnancy occurred during a period of low quality and quantity of forage on offer. This gave rise to somewhat higher death rates in pregnant does. Although not yet documented in goats, the appearance and continuation of oestrus activity and/or ovulation and fertilization rates in this case may have been negatively affected by the development of excessive body condition before mating. Likewise, poor pre-mating range condition, as observed in group 5, was probably not responsible for the predicted depression in performance. Rather it was due to a drastic increase in prenatal wastage during late pregnancy, which seemed to be related to rapid changes in forage quality at the onset of the long rains in February-March.

Although at a substantially lower level, fecundity rates showed a trend with increasing parity similar to that reported previously by Adu et al. (1979) for Red Sokoto goats. The authors provided estimates up to the third kidding at which stage goats produced on average 2.0 kids per parturition; about 60 percent more than in the present study. Results of the present analysis suggest that this trend in fecundity rates can, to a large part, be attributed to the effect of physiological maturity on litter size. There is a paucity of performance data concerning fecundity rates in African goat breeds. Nonetheless, it can be concluded that reproduction does not seem to constitute an acute problem in the SEA goat type studied in this work. Moreover, the statement made by Peacock (1984) that the attempt of Maasai herders to restrict breeding to the months of July and August is an "artificial obstacle to reproduction" (p.361) does not seem to be unequivocally true. In the present experiment, the overall average fecundity rate, adjusted for parity, was 1.18 kids per does exposed. This is the average reproductive performance which one could expect to observe upon implementing an aseasonal breeding regime consisting of joining an equal number of does in each of the six consecutive mating seasons. By comparison, there was some evidence that restricting breeding to a period at the onset of the long rains is likely to result in a larger kid crop per doe exposed (1.46), and with 1.07 to 1.23 kids born per doe exposed even mating during the long dry season failed to exhibit the deleterious impact on reproductive performance advocated by Peacock (1984).

Weaning rate

The ranking of weaning rate for the six mating season groups differed markedly from that of fecundity rate due to large differences in postnatal kid survival. It should be stressed, however, that the reported estimates of weaning rates can be biased downwards, because no adjustment for censored observations was made in calculating this criterion. In principle, weaning rate is a function of fecundity and kid survival to weaning, the latter estimates being affected by kids lost to follow-up with no information about their survival status at the time of weaning. Although the number of censored observations was small, their effect on estimates of weaning rate are difficult to quantify and, hence, these results should be interpreted cautiously. With 1.11 kids per doe exposed, the largest litter size at weaning tended to be produced by goats mated at the peak of the long dry season (mating season group 4). By comparison, the aseasonal breeding regime described above could be expected to produce, on average, 0.91 kids at weaning per doe exposed, thus pointing to the fact that the restricted breeding management practised by Maasai herders in southern Kenya might indeed be beneficial.

Clearly, mating during the short dry season should be avoided (mating season group 1), since here large pre-weaning losses are likely to severely depress the number of kids weaned per doe exposed. In the latter group,

about half of the kids born died before weaning. This leads to the rather obvious conclusion that real improvements in goat flock performance cannot be achieved by concentrating efforts solely on increasing reproductive performance. Such improvements can only be obtained upon integrating the whole production process, for which kid survival is of paramount importance (Delgadillo & Malpaux, 1996). Kid survival not only affects the number of surplus animals available for offtake, but also the number of female youngstock available as replacements. Reduced availability of replacements imposes restrictions on selective culling of less productive animals, which is instrumental in achieving and maintaining the most productive demographic structure in the breeding herd.

2.5 Conclusions

The results of this study indicated that seasonality in the availability and quantity of forage on offer as it prevails throughout northern Kenya can have significant impacts on individual reproductive traits in SEA goats. The most pronounced influence, as captured by the subjective phenological pasture condition scores, was detected in relation to prolificacy and fecundity rates. The observance of the latter effect was a direct consequence of the fact that litter size is one of the determinants of fecundity as defined in this work. The mating season treatment effect, however, could not be shown to have a statistically significant effect on reproductive traits. Though the range of predicted values for traits such as conception and prolificacy rates among mating season groups were quite large, the inter-year variability in seasonal environmental conditions were too high to permit a clear expression of statistical differences between individual groups with respect to the traits considered. Nevertheless, it appears that joining does during the short dry season, just before the onset of the long rains, could produce the largest number of offspring per doe exposed. But the results with respect to weaning rate indicate that this superiority is entirely lost due to high mortality in young kids during the following long dry season. To summarize, controlled breeding is most likely to be an inefficient management tool to improve reproductive performance of pastoral goat herds, as long as no remedy is found for reducing kid mortality until weaning.

Chapter 3

An analysis of survival curves in seasonally mated pastoral goat herds in northern Kenya using logistic regression techniques

3.1 Introduction

The biological productivity of livestock herds is determined by the three fundamental processes of reproduction, growth and development, and death (Konandreas & Anderson, 1982; Baptist, 1992*a*; Upton, 1993). Insufficient reproductive performance and excessive mortality have been found to impose severe restrictions on goat production in semi-arid regions of Africa (Hinch et al., 1985; Traoré and Wilson, 1988; Ba et al., 1996; Ndlovu & Simela, 1996). This is because these two components are themselves determinants of herd dynamics over time and, hence, of sustainable rates of offtake and selective culling per time unit (Nugent III & Jenkins, 1993). Moreover, they have a major influence on the (stable) structure of goat flocks in terms of the proportion of male and female kids, surplus stock, replacements, and breeding animals, and thus on the type and quality of offtake that can be obtained.

Environmental factors such as climate and season of year have a strong influence on reproductive performance and survival in pastoral goat herds. It has often been argued that the effects of fluctuating nutritional levels on both components could be reduced by manipulating the reproduction process in such a way as to balance nutrient requirements of the herd with seasonal pasture forage production (Smith et al., 1982; Field et al., 1984; Lebbie et al, 1996). The previous chapter has shown that under the environmental conditions prevailing in northern Kenya improvements in reproductive performance achieved by a restricted breeding management can easily be nullified by excessive youngstock mortality during the preweaning period. Similarly Upton (1985) and Wilson et al. (1985) observed that the effect of improving survival on the productivity in small ruminant flocks is probably at least as great as that expected from increases in reproductive or productive performance. Adverse environmental conditions may either directly result in increased mortality through starvation or hypothermia, or indirectly by favouring the incidence of certain types of diseases (Sherman, 1987). The present chapter investigates survival in Small East African (SEA) goat flocks subjected to a management intervention which limits breeding females to one parturition per year by imposing a single short breeding period. The aim is to identify that period within the year during which breeding optimises survival of youngstock, immature surplus and replacement stock, and breeding females. Given that developmental processes cause individual animals to differ in their susceptibility to death, it is necessary to further differentiate these broad herd categories. Relevant categories include age, body weight, and parity of dam. Data are provided which show how mortality changes as animals move through these successive life-cycle stages.

Ordinary statistical techniques such as analysis of variance or multiple regression are not well suited to the analysis of event-history data such as survival of animals over a given follow-up time period. Follow-up time intervals of interest in analysing survival of does and youngstock range, respectively, from mating until time at rebreeding, and from birth until age of disposal or first breeding. Two typical features of time-to-event data, censoring and time-varying explanatory variables, create major difficulties for standard statistical procedures (Allison, 1995). Censoring occurs when the event of interest (death) has not been observed for a number of individuals or when individuals have been "lost to follow-up" with no information about their survival status at the time of the analysis. Explanatory variables that change in value over the observation period often relate to environmental factors, such as pasture forage production. In this study, an approach using logistic regression techniques and polynomial spline functions is applied to parametrically estimate hazard rates and survival curves from censored data. The approach is particularly useful for accomodating both time-dependent covariates as well as nonproportional hazards, that is, situations where the effect of covariates on the probability of death change over time.

3.2 Materials and Methods

Experimental data

Data for this study pertain to the results of an experiment conducted between January 1984 and January 1988 at the Ngare Ndare Research Station of the University of Nairobi in Isiolo District, northern Kenya. The climate is semi-arid, rainfall (long-term annual average at Isiolo township: 615 mm) being distributed over two distinct rainy seasons, a long rainy season from March to May, and a short rainy season from October to November. The vegetation can be characterised as a semi-arid thornbush savannah dominated by various Acacia species with a sparse groundcover of annual grasses, herbs, and soft dwarf shrubs.

The experimental design and herd management were described in detail in Chapter 1. Briefly, 145 does of the SEA type were maintained under simulated pastoral management conditions and used for a total of 381 exposures which were distributed among 18 consecutive breeding groups consisting of approximately 18 does each. The only interventions with the pastoral management were vaccination for Contagious Caprine Pleuro-Pneumonia and the strategic use of an anthelmintic. A buck was introduced into each of the 18 breeding groups for a period of two months duration and was thereafter transferred to the next group, so as to achieve year-round mating, kidding, and weaning. Weaning occurred at 16 weeks of age. Three complete production cycles, ranging from mating until the time at which youngstock had reached an age of two years were obtained for five of the six consecutive two month breeding periods per year generated by the experiment. The sixth period had only two complete cycles, because the last breeding group of the experiment, which was set up in December 1986, had to be discarded due to incomplete records. The experimental treatment thus consisted of six mating periods or seasons, the first taking place from February to March (labelled as mating season 1) and the sixth taking place from December to January (mating season 6). Mating seasons 4 and 5 (August to October, and October to December) had to be assumed to have taken place over a period of three months due to a delay of one month which occurred in setting up the first breeding group of mating season 4 in 1984.

Measurements of liveweight of all animals and milk production of does were taken at two-weekly intervals. All events such as abortion, birth, and death were recorded continuously. A total of 8547 recordings were obtained on survival, liveweight, and milk production of does; 9837 observations were available on survival and liveweight development of youngstock. Whenever possible dead animals were subjected to a post mortem examination to attempt to establish the cause of death. The initial classification of causes of death included: unexplained loss, predation, doubtful diagnosis, miscellaneous causes, pneumonia, emaciation, cestodes, and stongyles. Pasture condition was judged every two weeks using a subjective phenological pasture condition score ranging from 1 to 4 based on greenness and abundance of the herblayer (range condition score [I]), including grasses, herbs, and small dwarf shrubs. The condition score for the herblayer was upgraded to a maximum score value of 5 to integrate the contribution of bushes and trees with regard to browse availability and the production of high quality litter such as leaves, flowers and fruits (range condition score [II]).

Data preparation

Survival of kids was studied at 2 week intervals from birth to 104 weeks of age, for a total of 57 follow-up time intervals. The method of statistical analysis used for estimating survival rates required creating a data set in which each animal had a separate record for each follow-up time interval it was observed in the study (see below). The dichotomous dependent variable was coded as zero when the animal survived or was censored in (i.e., withdrawn from the study for some reason other than death) a given time interval, and one when it died. All abortion records were omitted from the analysis of kid survival, whereas still birth events were considered to represent valid death events that occurred at the beginning of the first time interval of follow-up. Emergency culls were treated as censored observations.

The data on doe survival were also converted into a format with one record per animal per time interval on study. Doe survival was investigated over a period of 70 weeks from mating. As before, a biweekly time step was chosen, resulting in a total of 35 follow-up time intervals. Does which were allocated to a new breeding group before the 70 week period elapsed were considered to have been lost to follow-up at the time of rebreeding. Likewise, all forced cull events were labelled as censored observations. Note that follow-up time was not synchronized to parturition date. However, average time from the start of the mating period until parturition for fertile does that did not abort was 22.3 weeks (±2.5) and did not differ significantly between mating season groups. Therefore, the distribution of time at weaning was centred around 38 weeks from the origin, i.e. the onset of the respective mating period.

Statistical analysis

For the purpose of describing the approach adopted to estimate survival rates, suppose that a set (t_i, w_i, $\mathbf{X}_i$), i=1,..., n, of independent observations is obtained from n individuals, where t_i is the time an individual is known to have survived before the event, w_i=1 if the individual died at t_i, w_i=0 if the individual was censored at t_i, and $\mathbf{X}_i$ denotes a vector of known explanatory variables. Let T represent the random variable specifying time until death. Then the probability $S(t,\mathbf{X}_i)$ that an individual with covariate vector $\mathbf{X}_i$ dies after time t is defined as

$$S(t,\mathbf{X}_i) = \Pr(T>t|\mathbf{X}_i) = 1-F(t, \mathbf{X}_i) \text{ ,}$$

where $F(t, \mathbf{X}_i)$ is the cumulative distribution function for t given $\mathbf{X}_i$. The function $S(t, \mathbf{X}_i)$ is called the *survival function*, and is related to the *hazard function*, $h(t, \mathbf{X}_i)$, by the equation

$$h(t, \mathbf{X}_i) = f(t, \mathbf{X}_i)/S(t, \mathbf{X}_i) \text{ ,}$$

where $f(t,\mathbf{X}_i)$ is the probability density associated with $F(t,\mathbf{X}_i)$. The hazard function is also called the force of mortality at t, since it represents the instantaneous risk of death at t, given that the individual has survived to time t (Laird & Oliver, 1981). The hazard function can be expressed as a function of both time and the explanatory variables, and allows the investigation of the effects of these variables on survival.

Allison (1984), Efron (1988), and Gillespie et al. (1994) proposed the using of standard logistic regression techniques to estimate hazard rates and survival curves from censored data. The general form of the model for an individual i is given by (Efron, 1988)

$$\lambda_i = \ln[p(\mathbf{X}_i)/(1-p(\mathbf{X}_i))] = \mathbf{X}_i\beta \text{ ,}$$

where $p(\mathbf{X}_i)$ and λ_i are the probability and log-odds, respectively, of an individual with covariate vector $\mathbf{X}_i$ dying in a given time interval. The probability $p(\mathbf{X}_i)$ corresponds to the discrete hazard as a function of the covariate vector $\mathbf{X}_i$. Given estimates, $\hat{\beta}$, of the parameters, the hazard rate $p(\mathbf{X}_i)$ can be estimated from the inverse logit function:

$$\hat{p}\,(\mathbf{X}_i) = 1 / [\,1+ e^{-\hat{\lambda}_i}]$$

In order to use logistic regression with survival data, the set (t_i, w_i, $\mathbf{X}_i$), i=1,..., n, of observations on n individuals must be expanded so that each individual has a separate record for each time interval it was observed in the study (Allison, 1984). Each individual thus contributes a number observations to the analysis which is equal to the number of time intervals until it died or was censored. The response variable is dichotomous, indicating whether the individual died or not in the interval. To simplify notation, the index i for individuals is omitted in what follows. Let j, j=1,...,N, be the index for a follow-up time interval of unit length, where N is the last time interval considered in the analysis, and h_j represent the discrete hazard rate of an individual dying in the jth time interval given that it has survived until the beginning of the jth interval. For each value of j, let $\mathbf{X}_j$ be a known 1×p covariate vector. The logistic regression model then is

$$\lambda_j = \ln[h_j/(1-h_j)] = \mathbf{X}_j\beta \text{ , } j=1,...,N$$

with β being a p×1 vector of unknown parameters. Cubic spline functions in time can be used to estimate the hazard function of an individual dying in a given time intervall. Polynomial splines are piecewise polynomials satisfying continuity constraints at points joining the pieces, which are called knots (see Smith (1979) for further details). When a cubic spline function in time with a knot at time t, without restrictions on smoothness of the join, is to be fitted to the hazard rate, the covariate vector $\mathbf{X}_j$ can be written as

$$\mathbf{X}_j = (1,\ t_j,\ t_j^2,\ t_j^3,\ (t_j-t)_+^0,\ (t_j-t)_+^1,\ (t_j-t)_+^2,\ (t_j-t)_+^3)\text{ ,}\quad j=1,...,N$$

where

$(t_j-t)^m_+=(t_j-t)^m$ if $t_j-t>0$, and

$(t_j-t)^m_+=0$ if $t_j-t\le 0$, m=0, 1, 2, 3.

Fitting a logistic regression based on the above specification yields a completely separate cubic function on either side of the knot at t. Including indicators for treatment and classification effects in the design matrix is straightforward. Upon multiplying each time and/or "+function" term by an indicator, different response

functions over time are obtained for each level of the respective treatment (i.e., mating season) or classification effect. Determining the order of the polynomial segments as well as the continuity restrictions and covariate interactions required to achieve a satisfactory fit can be done using standard multiple regression hypothesis testing methods (Smith, 1979). Logistic regression models can be fitted to survival data using the generalized linear model approach (McCullagh & Nelder, 1983).

Maximum likelihood estimates of the survival curve, G_i, are obtained using estimates of the hazard rates, $\hat{h}_i$,

$$\hat{G}_i = \prod_{1<j<i}(1-\hat{h}_j)$$

The procedure GENMOD (SAS Release 6.12, 1996) allows the fitting of binary outcomes to a mixture of continuous and categorical explanatory variables, and was used in this study to estimate hazard rate curves. As a first step, the general form of the cubic spline function in time was investigated by plotting the life-table hazard-rate estimates, $\hat{h}_j = s_j/n_j$, where s_j and n_j are the total number of deaths and the total number of individuals present at time j, respectively, against follow-up time.

In general, deciding on the number and position of the knots, and the order of the polynomial in each segment is not simple (Montgomery & Peck, 1982). No more than three knots were identified for estimating preliminary model versions, because the great flexibility of spline functions makes it very easy to overfit the data. The knots were selected such that extreme points were centred in each segment and the inflexion points were located near the knots. Final knot positioning was carried out by fitting a series of models with different combinations of knot positions in proximity of the selected points, and identifying the model which produced the smallest deviance. The polynomial degree within each segment was determined based on the hypotheses testing procedure in partially ordered spline models given by Smith (1979). Selection of covariates among those given in Table 3.1 to be retained in final models was based on backward selection from a model including all possible interaction terms up to the third degree, with terms sequentially removed if the reduction in deviance, adjusted for all other terms in the model, was not significant at the 15 percent level.

Table 3.1. Definition of predictors included in initial models fitted to survival data.

Response	Fixed effects
Doe survival	• mating season (1 to 6) • parity at breeding (0; 1; 2; ≥3) • weight at breeding in kg (<25; 25 to 30; 30 to 35; 35 to 40;≥40) • reproductive status (empty; pregnant) • Lagged median range condition score [I] for the current and the two immediately preceeding periods (integer scores of 1 to 4) • Lagged median range condition score [II] for the current and the two immediately preceeding periods (integer scores of 1 to 5) • production cycle of the experiment (1 to 3) • time
Kid survival	• mating season (1 to 6) • birth weight in kg (<2; 2 to 2.5; ≥2.5) • total milk yield until weaning in kg (<22.5; 22.5 to 32.5; 32.5 to 42.5; 42.5 to 52.5; ≥52.5) • sex • litter size (single; twins) • parity of dam at breeding (0; 1; 2; ≥3) • lagged median RC scores [I] and [II] (as above) • production cycle of the experiment (1 to 3) • time

The bootstrap technique (Efron (1981), Rosenberg (1995)) was used to estimate non-parametric confidence intervals around survival curves. To apply the bootstrap, the spline model of interest was fitted to 1500

random samples taken with replacement from the observed sample data. Bootstrap confidence intervals (90 and 95 percent) for survival curves were generated from the bootstrap distribution of survival rate estimates with the bias-corrected percentile method (see Efron, 1987).

3.3 Results

3.3.1 Kid survival

Table 3.2 shows the causes of death by age category. In spite the fact that postmortem examinations were carried out on almost all animals that died during the experiment, in most of the cases (38 percent), the pathological findings on the carcasses were inadequate for a specific diagnosis. This was particularly true for animals dying within two weeks of birth. Another 15 percent of all death events were unexplained losses, but the majority of these can probably be attributed to animals that strayed and got lost from the herd and were ultimately eaten by predators. Taken together with the number of death events that were known to be due to predation, this would account for 28 percent of all deaths. Miscellaneous causes included injuries, poisoning, worm infections, metabolic disorders such as ruminal tympany, and deaths that occurred during a heavy storm in November 1987 (9 events). The incidence of emaciation was largely confined to the category of 2 weeks of age until weaning.

Graphical inspection of observed death rates in kids supported the conclusion that a polynomial spline function in time with two knots might provide sufficient flexibility to approximate mortality rates in young stock over the follow-up period of 104 weeks. The first knot was set at 20 weeks, and the second at 40 weeks of age. The final polynomial spline consisted of a third degree base function, a segment joining at t=20 containing a quadratic and cubic term, and a segment consisting of a quadratic term only, joining at t=40.

Dam parity (p>0.3), litter size (p>0.5), and sex of kid (p>0.5) did not exert significant influences on death rates. Birth weight, total milk yield until weaning, and lagged median range condition scores [I] and [II] were confounded with the mating season treatment effect. Therefore, two types of models were fitted, one including mating season and production cycle (model *a)* in Table 3.3), and the other, birth weight, total milk yield of dam until weaning, and the two range condition indices as main effects. In the latter model, production cycle did not significantly affect hazard rates.

Table 3.2. Causes of age-specific juvenile and kid mortality.

Cause	Age in weeks <2	2 to 16	16 to 52	52 to 104	Number of events	Percent of total
Born dead	8	–	–	–	8	7%
Predation	3	5	6	1	15	13%
Pneumonia	–	1	–	–	1	1%
Malnutrition	–	15	2	–	17	14%
Doubtful diagnosis	20	6	13	6	45	38%
Miscellaneous	–	–	12	2	14	12%
Unexplained loss	1	6	9	2	18	15%
Number of events	32	33	42	11	118	
Percent of total	27%	28%	36%	9%		

Table 3.3. Analyses of deviance for final models fitted to data on kid survival.

Model*)	df	Residual deviance	Source	Scaled χ^2	df	$p>\chi^2$
a)						
Intercept	5173	1004.5				
+MS+PC+t+t^2+t^3+	5135	693.4	MS	4.96	3	0.175
$(t-20)^2_+$+$(t-20)^3_+$+$(t-40)^2_+$+			PC	17.03	2	<0.001
MS·[t+t^2+t^3+$(t-20)^3_+$+$(t-40)^2_+$]			t	8.77	1	0.003
			t^2	3.40	1	0.065
			t^3	2.67	1	0.102
			$(t-20)^2_+$	46.13	1	<0.001
			$(t-20)^3_+$	15.66	1	<0.001
			$(t-40)^2_+$	0.82	1	0.366
			t·MS	6.75	3	0.080
			t^2·MS	7.80	4	0.099
			t^3·MS	8.86	4	0.065
			MS·$(t-20)^3_+$	13.66	5	0.018
			MS·$(t-40)^2_+$	27.63	4	<0.001
b)						
Intercept	5173	1004.5				
+BW+MILK16+t+t^2+t^3+	5157	778.6	BW	13.68	2	0.001
$(t-20)^2_+$+$(t-20)^3_+$+$(t-40)^2_+$+			MILK16	28.79	4	<0.001
t·MILK16			t	34.22	1	<0.001
			t^2	27.78	1	<0.001
			t^3	25.64	1	<0.001
			$(t-20)^2_+$	20.32	1	<0.001
			$(t-20)^3_+$	26.71	1	<0.001
			$(t-40)^2_+$	12.40	1	<0.001
			t·MILK16	15.33	4	0.004
c)						
Intercept	3701	855.4				
+RC[I]+t+t^2+t^3+	3692	704.6	RC[I]	20.87	3	<0.001
$(t-20)^2_+$+$(t-20)^3_+$+$(t-40)^2_+$			t	28.42	1	<0.001
			t^2	21.98	1	<0.001
			t^3	20.05	1	<0.001
			$(t-20)^2_+$	10.62	1	<0.001
			$(t-20)^3_+$	15.77	1	<0.001
			$(t-40)^2_+$	21.04	1	<0.001

Table 3.3. (continued)

Model*)	df	Residual deviance	Source	Scaled χ^2	df	$p>\chi^2$
d)						
Intercept	3650	867.5				
+RC[II]+t+t^2+t^3+ $(t-20)^2_+$+$(t-20)^3_+$+$(t-40)^2_+$	3640	683.6	RC[II]	42.12	4	<0.001
			t	23.69	1	<0.001
			t^2	18.07	1	<0.001
			t^3	16.72	1	0.023
			$(t-20)^2_+$	9.31	1	<0.001
			$(t-20)^3_+$	13.66	1	<0.001
			$(t-40)^2_+$	17.55	1	<0.001

*) MS=matingseason; BW=birth weight; MILK16=total milk yield until weaning; PC=production cycle; RC [I] and [II]= lagged median range condition scores [I] and [II] at each observationtime point; t=follow-up time.

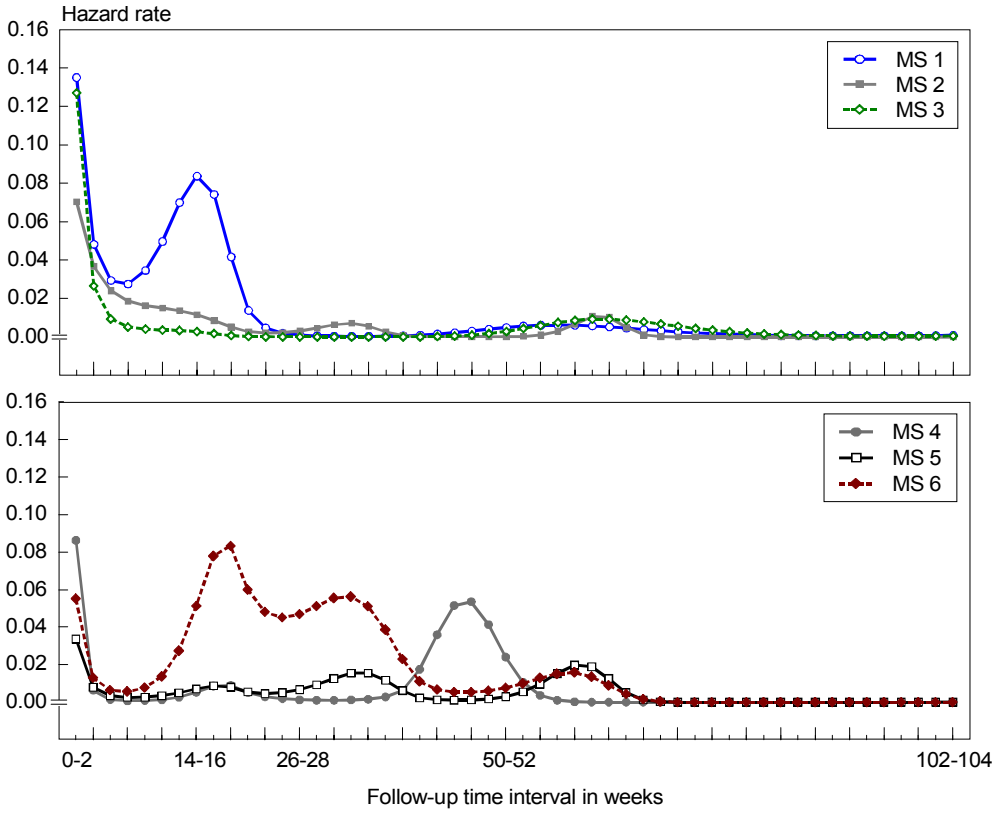

Figure 3.1. Estimated hazard rate curves by mating season (MS) for the data on kid survival.

However, a problem occurred in simultaneously estimating the effects of birth weight, milk yield, and range condition scores. The assessment of range condition was discontinued in November 1987, before kids born in early 1986 andthereafter had reached the age of two years. In order to avoid obtaining biased estimates due to the absence of range condition measurements for these observations, hazard rate profiles for the birth weight and milk yield effects were estimated without adjusting for the effects of range condition (model *b)* in Table 3.3). Finally, separate models were fitted to obtain hazard estimates for both range condition scores (models *c)* and *d)* in Table 3.3).

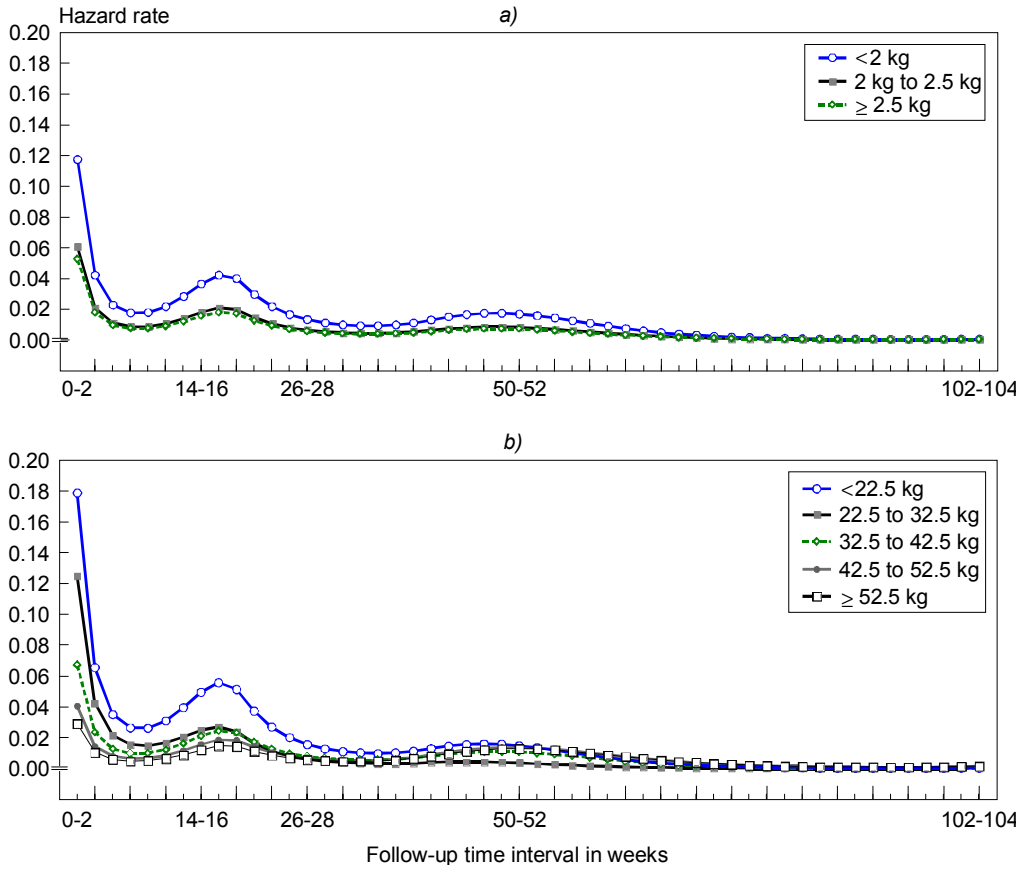

Figure 3.2. Estimated hazard rate curves for the kid survival data, according to *a)* birth weight, and *b)* total milk yield of mother until weaning.

The highly significant interaction terms between time factors and mating season are a clear evidence of non-proportionality of death risks across mating seasons. A graphical display of incidence rates by mating seasons is shown in Figure 3.1. The response profiles show relatively high perinatal death rates in all mating season groups. Newborns were exposed to the highest risk of death when born just after the long rains (mating season 1), at the end of the long dry season (mating season 3), or during the short dry season (mating season 4). Significant differences in incidence rates within two weeks from birth were found between mating season groups 1 and 5 ($p< 0.05$), with an estimated odds-ratio of 4.5. In the latter group, kids were born during the long rains.

A noticeable rise in hazard rates was observed around the time of weaning at 16 weeks of age in mating season groups 1 and 6. In both cases, weaning took place during the long dry season, under unfavourable forage conditions. Kids in mating seasons 1 and 6 were, on average, exposed to 15.5 and 9.2 times higher risk of death, respectively, at 16 weeks of age than kids in all other groups ($p< 0.01$). Inadequate nutrition continued to cause higher death rates in the former two groups well beyond the weaning period. This is particularly true for mating season group 6, in which mortality rates remained above 4.5 percent per time period, and differed significantly ($p< 0.05$) from those in all other groups, until 28 weeks of age. The following rise in incidence rates at about 34 weeks in the latter group, as well as the conspicuous peak at 48 weeks in the hazard curve of mating season 4, were both due to the joint occurrence of an extended dry season period with poor range conditions until the end of October in 1987, and of a heavy rain storm in the following month, during which 4 out of the 8 kids present at that time in group 6, and 6 out of the 21 kids exposed in group 4 died. It should be emphasized that the hazard rate estimates for mating season 6 might have been biased upwards due to the smaller sample size. Nevertheless, the effects of inadequate nutrition on incidence rates appeared to be much less pronounced in mating seasons 2 to 5.

With respect to the production cycle main effect, the overall risk of death was approximately 2.7 and 1.8 times higher in the first than in the second and third cycle, respectively ($p< 0.05$). This was caused by a prolonged dry period which prevailed from July to November in 1984. Overall hazard rates in the second were similar to those in the third production cycle, with an estimated odds ratio of 0.7.

Although significant differences in hazard rates between total milk yield levels until weaning were detected, they seemed to have a much less detrimental effect on kid survival than mating season (Figure 3.2). The same holds for the effect of kid birth weight. Milk yield levels had, however, a marked influence on perinatal survival rates. Insufficient milk production (< 32.5kg until weaning) led to very high kid mortality during the first two weeks of life (Figure 3.2*b*). Predicted hazard until 2 weeks of age was as high as 17.9 and 12.5 percent for kids born to does with a total milk yield until weaning of less than 22.5 kg, and of 22.5 to 32.5 kg, respectively. These figures differed significantly at the 5 percent level from those obtained for higher yield levels. Hazard rates reached a peak just after weaning, and were again found to be much higher in kids receiving very low quantities of milk (< 22.5 kg) during the suckling period than in those receiving at least 22.5 to 32.5 kg milk ($p< 0.05$). This difference remained significant until 28 weeks of age.

Kids born to dams producing 52.5 kg or more milk during the suckling period were exposed to the lowest overall risk of death. By comparison with the lowest milk yield level (< 22.5 kg), the chances of dying within 2 weeks of birth and at weaning were, respectively, 7.2 and 4.3 times lower. Due to the interaction of the milk yield main effect with the linear time term, differences between milk yield levels disappeared, and some of the hazard curves began to cross, after week 34 of the follow-up time period. This indicates that beyond this time point, other factors became more important in determining kid survival than milk yields.

The effect of birth weight on incidence rates did not change with age due to the absence of interactions with time factors in the fitted model. The relative differences between the three hazard rate curves shown in Figure 3.2*a* thus remained constant throughout the observation period. Kids born with less than 2 kg were exposed to a much higher risk than kids weighing 2 to 2.5 kg ($p< 0.01$) and more than 2.5 kg at birth ($p< 0.01$). The corresponding odds of death were estimated to be 2.1 and 2.4 times higher in the lowest birth weight class.

The hazard ratios (or odds ratios) for the levels of both range condition scores remained constant throughout the observation period, as indicated by the lack of interactions between these risk factors and time covariates in models *c)* and *d)* in Table 3.4. Note that RC [I] and [II] were time-dependent risk factors that changed in value over time (i.e., with increasing age) for an individual observation. Therefore, proportionality of the odds for any two values of each of the range condition scores implied that the effect of median forage quantity and quality on offer over a 6 weeks period on the probability of death in kids was independent of kid age. The odds of death associated with each level of the two range condition scores are reported in Table 3.4, along with the corresponding approximate relative risks between all score level pairs. For both range condition indices, the odds of death increased

Table 3.4. Estimated mean effects of range condition scores [I] and [II] on the odds of death in kids per two weeks time interval. Approximate relative risks (odds ratios) among score levels are given on the right.

		Odds*)	Relative risks of death				
				1	*2*	*3*	
RC [I]	1	0.0105^{a}	*1*				
	2	0.0066	*2*	1.6			
	3	0.0033^{b}	*3*	3.2	2.0		
	4	0.0027^{b}	*4*	3.9	2.5	1.2	
				1	*2*	*3*	*4*
RC [II]	1	0.0202^{a}	*1*				
	2	0.0129	*2*	1.6			
	3	0.0064^{b}	*3*	3.1	2.0		
	4	0.0028^{b}	*4*	7.3	4.6	2.3	
	5	0.0028^{b}	*5*	7.2	4.6	2.3	1.0

*) Estimates without common letters in their superscripts differed at the five percent level of significance.

Table 3.5. Estimated probabilities and 95 percent bootstrap confidence intervals of kids surviving to selected time points, according to mating season, birth weight, and milk yield until weaning.

Term	Follow-up time (weeks)*) 2	16	52	104
Mating season				
1	0.865	0.562^{a}	0.515^{a}	0.486^{ac}
	[0.788; 0.930]	[0.459; 0.664]	[0.408; 0.630]	[0.374; 0.598]
2	0.930	0.804^{b}	0.770^{b}	0.742^{b}
	[0.847; 0.986]	[0.704; 0.886]	[0.652; 0.861]	[0.625; 0.856]
3	0.873	0.825^{b}	0.815^{b}	0.744^{b}
	[0.775; 0.937]	[0.720; 0.913]	[0.710; 0.900]	[0.629; 0.847]
4	0.914	0.890^{b}	0.677^{ab}	0.674^{bc}
	[0.841; 0.968]	[0.809; 0.951]	[0.561; 0.780]	[0.557; 0.777]
5	0.966	0.928^{b}	0.826^{b}	0.760^{b}
	[0.906; 1.000]	[0.849; 0.980]	[0.705; 0.914]	[0.625; 0.872]
6	0.945	0.768^{ab}	0.410^{a}	0.381^{a}
	[0.860; 1.000]	[0.645; 0.881]	[0.266;0.566]	[0.239; 0.546]
Birth weight (kg)				
< 2	0.883	0.700^{a}	0.530^{a}	0.479^{a}
	[0.813; 0.926]	[0.575; 0.785]	[0.382; 0.651]	[0.330; 0.606]
2 to 2.5	0.940	0.839^{ab}	0.733^{b}	0.698^{b}
	[0.905; 0.961]	[0.782; 0.881]	[0.659; 0.800]	[0.612; 0.767]
≥2.5	0.948	0.860^{b}	0.766^{b}	0.734^{b}
	[0.915; 0.965]	[0.800; 0.897]	[0.682; 0.824]	[0.631; 0.796]
Milk yield until weaning (kg)				
<22.5	0.821^{a}	0.587^{a}	0.431^{a}	0.399^{a}
	[0.732; 0.888]	[0.473; 0.697]	[0.326; 0.551]	[0.284; 0.515]
22.5 to 32.5	0.875^{ab}	0.728^{ab}	0.651^{ab}	0.642^{ab}
	[0.808; 0.926]	[0.623; 0.814]	[0.531; 0.748]	[0.515; 0.741]
32.5 to 42.5	0.933^{bc}	0.819^{bc}	0.693^{b}	0.649^{ab}
	[0.868; 0.968]	[0.703; 0.899]	[0.571; 0.804]	[0.506; 0.764]
42.5 to 52.5	0.960^{bc}	0.878^{bc}	0.744^{b}	0.670^{b}
	[0.908; 0.981]	[0.796; 0.929]	[0.641; 0.856]	[0.538; 0.792]
≥52.5	0.971^{c}	0.908^{c}	0.787^{b}	0.709^{b}
	[0.941; 0.987]	[0.839; 0.956]	[0.689; 0.894]	[0.567; 0.835]

*) Estimates without common letters in their superscripts differed at the 5% level of significance.

markedly with decreasing condition score. The differences in the likelihood of death were more pronounced among the levels of the browse adjusted index RC [II] than among those of the herblayer index. Kids exposed to pasture conditions characterized by lagged median RC [I] and [II] scores of 1, which typically were observed at the peak of the long dry season, were, respectively, 3.9 and 7.3 times as likely to die at any age as when exposed to conditions characterized by RC [I] and [II] scores of 4 ($p< 0.01$). The protective effect of increasing pasture conditions levelled off at higher score levels, as indicated by the relative risks of 1.2 and 1.0 between RC [I] scores of 3 and 4, and between RC [II] scores of 4 and 5, respectively. Estimated survival probability for each level of the mating season, milk yield until weaning, and birth weight main effects are given in Table 3.5. With respect to mating season, the lowest kid survival rate until 2 and 16 weeks of age was observed in group 1. Although not significantly different, predicted survival rate in mating season group 6 until two years of age fell below even the 48.6 percent achieved in group 1, down to a very low level of 38.1 percent.

Perinatal survival rates increased when kids were born under favourable forage conditions, such as it tended to be the case for groups 4, 5, and 6. The timing of the pre-weaning period in relation to environmental conditions was a decisive factor in determining kid survival until weaning age. Almost 44 percent of the kids born at the onset of the long dry season (group 1) died before 16 weeks of age, a significantly larger figure than the approximately 11 and 7 percent observed in groups 4 and 5, in which weaning took place during and towards the end of the long rainy season, respectively. In the latter group, survival declined only slightly until the yearling stage. In contrast, conditional survival probabilities calculated from the figures in Table 3.5 revealed that 46.6 percent of the kids alive at weaning in group 6 were estimated to die until one year of age. (Note that these figures are conditional probabilities calculated from the results presented in Table 3.5). During the same period, substantial losses of 23.9 percent could also be observed in mating season group 4. The best performance until one year of age was achieved in mating season group 5 with 82.6 percent of the kids born surviving, followed closely by those born in groups 3 and 2 (81.5 and 77 percent, respectively). Mortality was less than 10 percent in all groups between one and two years of age.

Significant differences occurred between the three levels of the birth weight effect from 16 weeks of age (Table 3.5). Almost 12 percent of the kids born with less than 2 kg of body weight died within 2 weeks, whereas mortality rates in kids weighing more than 2 kg at birth were at most 6 percent. Substantial differences between the first versus the second and third birth weight levels were also apparent at subsequent ages. After one year from birth, approximately 47 percent of all kids born with less than 2 kg of body weight had died, compared to about 27 and 23 percent in the two other birth weight classes. Only minor differences were observed throughout the follow-up time period between levels 2 and 3.

The hazard rate profiles for milk yield levels until weaning depicted in Figure 3.2*b* translated into very low probabilities of survival for kids which received less than 22.5 kg milk, and maximum survival probabilities for kids whose dams produced more than 52.5 kg milk, although still about 21 percent of the kids died within one year from birth in the latter group. Overall, a slightly curvilinear trend in survival rates over the five milk yield classes was observed. Significant differences ($p< 0.05$) were found between the first and the third to fifth yield classes, and between the second and fifth yield class until 16 weeks of age. The latter difference vanished after weaning, whereas the former persisted until the end of the observation period. The effect of milk yield levels upon pre-weaning mortality in kids was substantial, ranging from 9.2 percent in level 5 to 41.3 percent in level 1. As may also be seen from the profiles in Figure 3.2*b*, differential effects of milk yield on survival began to weaken after 28 weeks.

3.3.2 Doe survival

Of the 287 does exposed, 28 or roughly 9.8 percent died during the course of the experiment. In most of the cases (36 percent), postmortem examinations were inconclusive with regard to the cause of death. Taken together, unexplained losses and predation accounted for another 35 percent of all death events. Only three does died from pneumonia, three from starvation and two from miscellaneous causes.

The hazard function of an individual doe dying in a given follow-up time interval was approximated through a polynomial spline function in time consisting of a second degree base function, a segment joining at 28 weeks containing a quadratic and cubic term, and a segment consisting of a quadratic and cubic term joining at 38 weeks (Table 3.6), at which time most of the kids were weaned. Body weight at breeding, litter size, lagged live weight at each time point, as well as lagged median range condition scores [I] and [II] did not exert any significant influence on death rates. Doe survival was finally evaluated in terms of mating season, production cycle, parity, and reproductive status (fertile or empty).

The relatively small number of death events and their unequal distribution among mating season groups led to estimation problems. For instance, it was not possible to obtain separate hazard rate estimates for mating seasons 4 and 5. This was due to the fact that only two incidences had occurred in each of these treatment groups at the lower and upper ends of the follow-up time scale. Observations from both groups were therefore pooled before fitting logit models to doe survival data. Also, too few animals in parity stage four and greater survived beyond 26 weeks so as to preclude obtaining reliable hazard rate estimates, and does in this class weretherefore grouped with those having three prior kiddings. Significant interactions were found between time factors in the model and the main effects of mating season and reproductive status, indicating non-proportionality over time of death risks across the levels of these variables. In contrast, the influence of parity number on hazard rates remained constant over time.

Estimated hazard functions for pregnant and barren revealed that mortality was highest in does that failed to conceive, reaching a peak value of 0.01 during the time interval 16 to 18 weeks from the onset of mating and declining gradually thereafter (Figure 3.3). For fertile does, the risk of death increased towards the end of the gestation period and attained its maximum value just prior or after parturition (20-22 weeks). Incidence rates declined slightly during the first weeks of lactation, but peaked again before weaning at week 34 to 36 of follow-up. Although not statistically significant, death rates in lactating does exceeded those observed in barren females from 30 weeks onwards. Significant differences ($p< 0.05$) in death rates between fertile and barren does were detected between the second and twentieth week. Over a reproductive cycle of one year duration, the average relative risk of death was estimated to be 2.3 times higher in barren than in fertile does.

Table 3.6. Analysis of deviance for the final model fitted to data on doe survival.

Model*)	Residual df	Residual deviance	Source	Scaled χ^2	df	$p>\chi^2$
Intercept	4621	320.4				
+MS, PC, PARC, RS,	4596	243.9	MS	15.7	4	0.004
$(t-28)^2_+$, $(t-28)^3_+$, $(t-38)^2_+$,			PC	9.8	2	0.008
$(t-38)^3_+$, t·MS, t·RS			PARC	6.7	3	0.081
			RS	10.5	1	0.001
			t	9.6	1	0.002
			t^2	9.4	1	0.002
			$(t-28)^2_+$	4.8	1	0.028
			$(t-28)^3_+$	5.8	1	0.016
			$(t-38)^2_+$	6.4	1	0.012
			$(t-38)^3_+$	5.7	1	0.017
			t·MS	23.3	4	<0.001
			t^2·MS	23.9	4	<0.001
			t·RS	7.4	1	0.007

*)MS=matingseason; PC=production cycle; PARC=parity; RS=reproductive status; t=follow-up time.

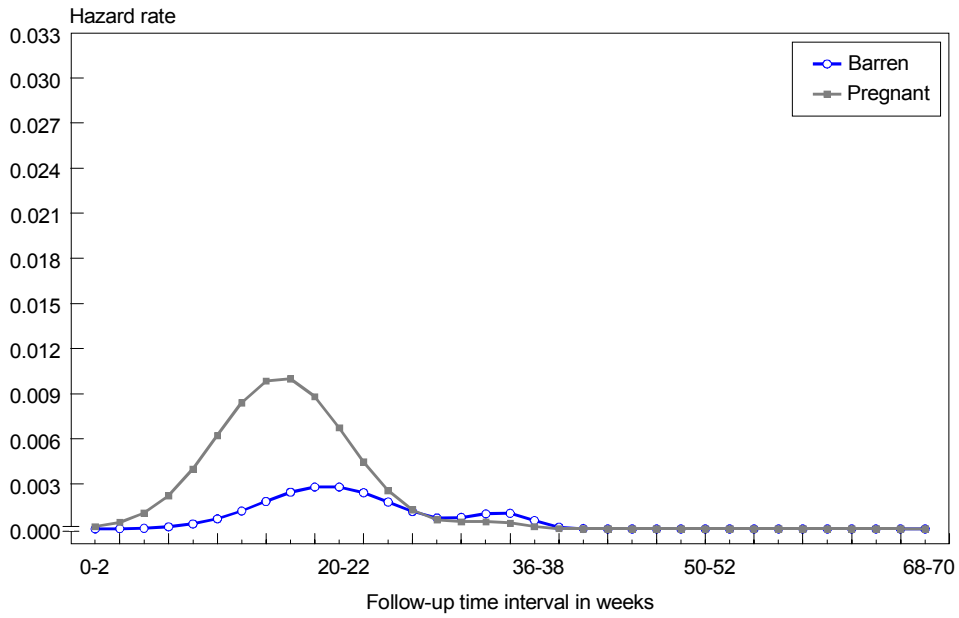

Figure 3.3. Estimated hazard rate curves according to reproductive status for the data on doe survival.

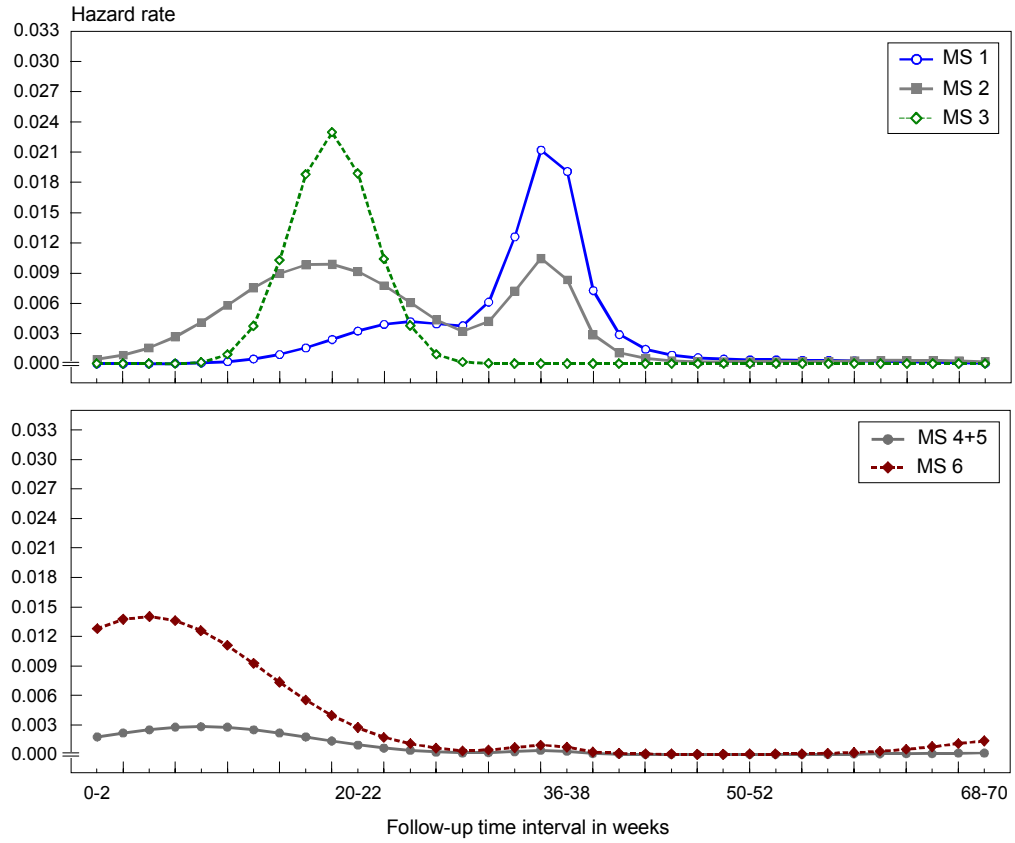

Figure 3.4. Estimated hazard rate curves according to mating season (MS) for the data on doe survival.

The shape of estimated hazard rate curves differed markedly across mating season groups (Figure 3.4). Relatively high death rates after the onset of mating and during the short dry season were observed in mating season group 6. Slightly elevated incidence rates during the same stage also occurred in groups 4 and 5, which were joined during and at the end of the long dry season, respectively. However, in the latter two groups, does were exposed to the lowest overall risk of death, and this also hold true for mating season group 6 after 22 weeks of follow-up. Only one animal died during the lactation stage in group 4, and none in groups 5 and 6.

A very different pattern in the distribution of death events emerged from the estimated survival time distribution for mating season groups 1 through 3 (Figure 3.4). In all three groups, mating occurred under favourable forage conditions, and incidences were concentrated either just prior to or immediately after parturition (group 3), at weaning (group 1), or during both of these stages (group 2). These peaks in hazard rates were related to the concurrence of production stages with high nutritional demands with poor forage conditions prevailing during the dry seasons. For instance, in mating season group 1, parturition occurred at the onset, and weaning toward the end of the long dry season. In the case of group 2, in which does had been joined two months later, parturition took place at the middle of the long dry season in August/September, whereas kids were weaned during the short dry season. The large increase in incidence rates around parturition time in mating season group 3 coincided with the end of the long dry season. However, unlike in the first two groups, none of the breeding females exposed died during the lactation stage, as is apparent from the sharp decline in the hazard rate curve after 22 weeks of follow-up. Significant differences in hazard rates were observed between mating season 3 and 4+5 from 16 up to 22 weeks. Between 30 and 50 weeks, hazard rate estimates in groups 1 and 2 were also found to be higher than in the latter group ($p< 0.05$).

First breeding females were exposed to the lowest risk. Although hazard rates increased linearly with the number of kiddings ($p< 0.05$), only very slight evidence was obtained for a significant difference in response between nulliparous does, and second and third breeding does ($p< 0.15$). All other differences between parity levels were non-significant. By comparison with first breeding females, the relative risk of death was estimated to be 2.6, 3.9 and 4.8 times higher in parity one, two, and three or greater does, respectively. Likewise to the analysis of kid survival, the highest mortality rates were observed during the first production cycle, and remained of similar magnitude during the second and third years of the experiment.

Estimated survival probabilities of does until selected time points as influenced by mating season, reproductive status, and parity are given in Table 3.7. As anticipated from the fact that only few significant differences in hazard rates were detected among the levels of these factors, the bootstrap confidence limits failed to reveal any significant differences in survival probabilities. Due to the relatively small number and sparse distribution of death events observed throughout the experiment, a much greater sample size would be required to isolate significant differences, if any, in doe survival across factor level means.

Survivability until 22 and 38 weeks in does that failed to conceive relative to those that did were estimated to be approximately 4.4 and 4 percent lower. Beyond 2 weeks of follow-up, mortality until completion of the reproductive cycle in both of these groups was predicted to drop to a low value of about one percent. The overall adjusted effect of reproductive status on doe survival thus was small compared to that of the mating season treatment.

The lowest survivability until the end of the reproductive cycle was exhibited by does mated in group 2, in which only 89 percent of the does exposed were expected to survive. The highest survival rate was achieved in groups 4 and 5, with an expected mortality rate of 2.6 percent until 52 weeks of follow-up. Survivability in mating group 6 was severely depressed due to the elevated incidence rates prior to 22 weeks. About 10.8 percent of the breeding females exposed in this group died before completing the reproductive cycle. The most severe reduction in survival rates during 22 and 52 weeks was experienced in mating season group 1, with an expected mortality rate over this time interval of 8.6 percent. Overall mortality rate in group 3 was predicted to be 8.8 percent, and thus was only slightly lower than in group 1.

Table 3.7. Estimated probabilities and 95% bootstrap confidence intervals of does surviving to selected time points by mating season, parity at breeding, and reproductive status.

	Follow-up time (weeks)		
Term	22	38	52
Mating season			
1	0.991 [0.948;1.000]	0.919 [0.805;0.991]	0.906 [0.742;0.978]
2	0.941 [0.832;0.985]	0.893 [0.741;0.969]	0.888 [0.729;0.966]
3	0.926 [0.820;0.975]	0.912 [0.784;0.970]	0.912 [0.784;0.970]
4+5	0.977 [0.910;0.996]	0.974 [0.906;0.995]	0.974 [0.905;0.995]
6	0.898 [0.635;0.992]	0.892 [0.618;0.991]	0.892 [0.616;0.990]
Parity			
0	0.990 [0.966;0.996]	0.987 [0.958;0.993]	0.987 [0.958;0.993]
1	0.975 [0.927;0.988]	0.966 [0.915;0.981]	0.966 [0.915;0.981]
2	0.963 [0.875;0.984]	0.950 [0.822;0.974]	0.949 [0.821;0.974]
≥3	0.954 [0.787;0.996]	0.938 [0.714;0.988]	0.937 [0.712;0.988]
Reproductive status			
Pregnant	0.988 [0.969;0.994]	0.978 [0.954;0.986]	0.978 [0.954;0.986]
Barren	0.944 [0.750;0.987]	0.934 [0.749;0.980]	0.934 [0.749;0.980]

Survivability over the reproductive cycle according to parity number, adjusted for the effects of mating season and reproductive status, ranged between 98.7 and 93.7 percent for first breeding and third or greater parity does, respectively. Estimated survival rates in does with one or two prior kiddings levelled of at approximately 96.6 and 94.9 percent beyond week 38.

3.4 Discussion

3.4.1 Kid survival

High rates of preweaning mortality in goats have been reported to be a major constraint on improving productivity in traditional goat husbandry systems (Devendra & Burns, 1983; Sherman, 1987; Wilson et al., 1985). Indeed, the analysis of reproductive performance (Chapter 2) has shown that the advantage of high fecundity may completely be lost through correspondingly high postnatal death rates in youngstock. High postnatal mortality incidence rates have been associated with, among other factors, sex of kid, multiple births, low birth weights and suboptimal feeding levels during gestation, parity and age of dam, low milk production, and season of birth (Adu et al., 1979;Gatongi et al., 1997; Gebrelul et al., 1994; Osuagwuh, 1991; Rattner et al., 1994; Wilson, 1984; Wilson et al, 1985). Unfortunately, all of these factors tend to be confounded to some extent, and they can therefore not be assessed simultaneously by entering them into the same statistical model. The main problem arising from such an analysis is that the effect of each variable cannot be interpreted as being free of effects of other collinear variables (Gillespie et al., 1994). For instance, the analyses performed with the present data indicated that dam parity affected litter size, milk yield level, and birth weight, while birth weight and milk yield level were, in turn, found to decrease with increasing litter size. The picture was further complicated by the fact that litter size, birth weight, and milk yield level of the dam varied with mating season (and, consequently, season of birth), which is an indicator variable that carries information on environmental and nutritional conditions prevailing at various stages of the reproductive cycle. It is thus hard to separate the individual contributions of these risk factors to kid morbidity and mortality. The strategy followed here was to assess the effect of those variables that were or could have been manipulated by experimental design, i.e. mating season and parity of dam, separately from that of observational variables such as litter size, birth weight, milk yield of dam until weaning, and range condition scores.

Parity of dam was not found to have a significant effect on mortality incidence rates. This contrasts with the findings of other studies conducted under comparable environmental conditions, which identified parity of dam to be a significant source of variation in kid mortality. For instance, Traoré and Wilson (1989), working with West African Sahel goats in Mali, found that kid mortality until 150 days of age decreased from 47.9 percent in first-born young to 26.1 percent at the fifth or later kidding. Similar differences between first and greater parity kids were also observed by Sacker and Trail (1966), and Wilson et al. (1984) and Gatongi et al. (1997), who studied mortality in SEA goat kids in Uganda and Kenya, respectively. The latter authors tested the effectiveness of two anthelmintic treatments applied either prior to or just after the onset of the rainy seasons on reducing kid survival until nine months of age. Based on the mortality rates reported by Gatongi et al. (1997), one can calculate that the anthelmintic treatments reduced the relative risk of death of first versus later parity kids from as much as 12.0 in the control group, to 2.3 and 5.2 in the two treatment groups. This effect was apparently mediated through an overall improvement in body condition of dams and birth weights of kids. In the present study, a deworming treatment was regularly applied to all animals prior to the rains, and, in light of the evidence provided by Gatongi et al., this may have contributed to the observed lack of association between parity of dam and kid survival. Furthermore, first breeding was delayed until does weighed at least 20 kg, leading to a mean liveweight at first conception of 26±4.7kg, and a mean age at first kidding of 90.1±12.97 weeks. The age of roughly 21 months at first parturition was markedly higher than that reported for other goat breeds in semi-arid Africa e.g., 16 months for West African Sahel goats (Wilson & Traoré, 1988), and 14.3 months for Red Sokoto goats (Adu et al., 1979). It was also much higher than the 14.7 and 15.5 months observed by Gatongi et al. (1997) in the two anthelmintic treatment groups noted above. Consequently, the corresponding liveweights at first conception of 21.9 and 20.9 kg were also considerably lower than those reported in the present study.

Both weight and age at first conception are generally considered to be important maternal factors influencing kid survival. Sherman (1987) ascribes the protective effect of doe age on kid survival to the positive correlation between age and liveweight of dam, which itself appears to be positively correlated with birth weights, as well as to the ability of older does to produce broader colostral immunity for kids. Supportive evidence for improved survival of first-born kids due to delayed age and increased weight at first conception is provided by Wilson (1984). In SEA goat flocks owned by Maasai herders, he found that first parity deaths were only slightly greater than the overall mean and attributed this finding to the management practices of the Maasai which are aimed at delaying age at first parturition.

The effect of litter size on kid survival failed to reach statistical significance after adjustment was made for the effects of birth weight and milk yield until weaning. Based on the present data, this finding was not unexpected since litter size could be shown to have a significant impact on both birth weight, growth rate, and milk yield until weaning. Both traits were found to be negatively affected in twin litters. As indicated previously, many workers found a significant effect of litter size on kid survival. However, since the effect of litter size is often assessed simultaneously with that of birth weight and parity of dam, interpretational difficulties arise because of the inevitable correlation between these factors (Hinch et al., 1985). The present results suggest that the primary risk factors are birth weight and the amount of milk supplied by the dam, rather than litter size per se. The risk of death for kids born under 2 kg was more than twice as high as that for kids weighing more than 2 kg at birth; and it is worth noting that this effect did not disappear with increasing age. Rattner et al. (1994) observed a similar constancy of the effect of low birth weight on survival in a study of kid mortality under semi-extensive management in Israel. Based on the mortality figures reported by Rattner et al. (1994) for three consecutive time periods ranging from birth to 48 hours, from 2 to 70 days, and from 70 days to six months of age, the risk of death for kids weighing up to 1.5 kg can be calculated to be 7.6, 2.2, and 2.0 times higher, respectively, than that for those kids weighing more than 1.5 kg at birth.

Low birth weight has consistently been identified by most workers as a major contributing factor to mortality in kids, especially during the early stages of life (Devendra & Burns, 1983; Sherman, 1987). The most likely cause of the increased vulnerability of kids with decreasing birth weight is the reduced fitness and inability of such kids to ingest adequate amounts of colostrum and milk, which subsequently further lowers their resistance to environmental stresses and infectious agents; this may lead to chronical unthriftiness and slow growth. Typically, deaths in these animals cannot be attributed to any specific cause, as was also the case in the present study. For 38 percent of all observed kid losses, no clear diagnosis could be established. Often, these events are thought to be related to the so-called starvation-mismothering-exposure (SME) complex which, according to Haughey (1991), can be considered to be the most important cause for nonspecific deaths in the first two weeks of life. The present data revealed that about 33 percent of all recorded death events occurred within this period.

The estimated hazard curves by milk yield class clearly demonstrated the importance of early nutrition for kid survival. Kids born to does producing less than 22.5 kg of milk until weaning were exposed to a particularly high risk of death during the first two weeks of life. But in contrast to birth weight, the effect exerted by the amount of milk available to kids diminished with increasing age. For instance, the predicted risk of death in the lowest milk yield category was 6.1 times as high as that in the highest yield category (>52.5 kg of milk) over the first two weeks of life, but subsequently this estimate declined to 4.2 around the time of weaning, and to 1.2 at one year of age, i.e., a relative risk that is close to independence. A possible explanation for this pattern is that kids born to low milking does were able to compensate for the restriction in milk availability by starting to graze on pasture forage at an early stage. Nevertheless, in absolute terms the difference in predicted survival probability between the lowest and highest milk yield class was tremendous. While in the latter case losses of only 2.9 and 9.2 percent were expected to occur over the first two weeks of life and until weaning, respectively, about 17.9 and as much as 41.3 percent of the kids nursed by low milking does were estimated to die over these two periods. This underlines the strong protective effect of an adequate milk supply under extensive management conditions. Well nourished kids are not only more resistant to pathogens, but are also less likely to be lost due to wandering and predation. Unexplained losses and predation, which together accounted for 28 percent of all losses, can be expected to be greater in kids weakened by malnutrition and starvation.

Although, as demonstrated by the analysis of lactation performance, some does were intrinsically low yielders, by far the most important source of variation in milk yields under semi-arid conditions is undoubtedly the plane of nutrition of dam during late pregnancy and lactation. Similarly, birth weight of kids is influenced by nutritional status of the dam at breeding and throughout the gestation period. Nutritional conditions around breeding time may also exert an indirect influence on birth weights by affecting ovulation rate, and thus litter size. Consequently, though in the present study birth weight and milk yield until weaning appeared to be strong predictors of death risk of kids, ultimately, these factors were themselves related to seasonal fluctuations in availability and quality of forage. This relationship was expressed through the observed differences in birth weight and milk yield until weaning across mating season groups. The resulting patterns of death hazard in youngstock suggest that synchronizing nutrient demands of the herd with forage production from pastures by manipulating mating season and, hence, season of birth, is possibly an effective strategy for reducing youngstock mortality in the current production system.

In accordance with the results reported by Wilson et al. (1985) from the study on Maasai SEA goat flocks referred to previously, maximum kid losses until weaning occurred when the entire period from birth to weaning coincided with the long dry season (mating season 1). The authors estimated pre-weaning mortality

in kids born during the dry season at 40.6 percent, which is almost identical to the 43.8 percent estimated for mating season 1. The hazard function for mating season 1 revealed that these losses were caused by very high incidence rates during the first two weeks of life and around the time of weaning. Taking into account the fact that 75 percent of all deaths events occurred during periods of low quality and quantity of forage on offer (i.e., scores of 1 and 2 of RC [I]), it can be inferred that the nutritional stress imposed on dams and their progeny in this group was to a large extent responsible for these excessive mortality rates. For the same reason, high perinatal death rates were observed in all groups in which dams delivered during the long (groups 2, and 3) or short dry season (groups 4), but declined noticeably when kids were born at the onset or at the middle of the long rainy season (groups 5 and 6). Does freshening during the latter period had higher levels of nutrition and were able to sustain a higher level of milk production than does kidding in the dry season. Nevertheless, one could expect the prevalence of infections with gastro-intestinal parasites and bacterial diseases to increase sharply during the rainy season, and to observe a concomitant increase in the number of youngstock succumbing to infectious diseases. However, death incidences due to worm infections and pneumonia, in particular, were very low throughout the experiment. This was also reflected in the fact that the predicted death risk decreased dramatically with increasing range condition score, irrespective of kid age. Therefore, it seems reasonable to conclude that the health care programme was very effective in controlling diseases which are generally a major source of kid losses during the rainy season, such as CCPP and helminthiasis. With respect to helminthiasis, this conjecture accords with the results of the study by Gatongi et al. (1994) noted above, that showed the anthelmintic treatment administered before the rains to reduce kid mortality rate in the first nine months of life to less than half the rate observed in the control group.

Similarly to mating season 1, weaning was also found to be a critical stage in mating season 6. The sharp increase in death hazard during August/September, at the peak of the long dry season, was probably caused by declining body condition of dams, decreasing levels of milk production, as well as by an absolute lack of available feed for the young themselves. In contrast, the stress of weaning did not appear to be associated with major losses when kids were weaned between the months of December and May, as was the case in mating seasons 2, 3, and 4. Higher pre-weaning levels of nutrition of dams and kids, coupled with the protective effect of the health care programme, seemed to have considerably decreased the susceptibility of youngstock to disease and mortality. Much in the same way, these factors apparently kept incidence rates at a low level even when kids were weaned at the onset of the long dry season (mating season 5). Similar findings were previously reported by Traoré and Wilson (1988) for agro-pastoral systems in Mali, and Wilson et al. (1985) for Maasai pastoral goat flocks in Kenya. In the latter study, pre-weaning mortalities for kids born during the short rainy, short dry, and long rainy season were estimated at 34.4, 25.5, and 17.5 percent, respectively. By comparison, the rates of 17.5, 11.0, and 7.2 percent estimated in the current experiment for mating season groups 3, 4, and 5, respectively, were consistently lower. Again, the health care programme carried out in the present study might partly account for the difference in the pre-weaning mortality levels.

In conclusion, confining mating in the current goat production system to the period between June and November is likely to confer a distinctive advantage in terms of youngstock survival. Such a strategy can be expected to yield maximum probabilities of survival to one year of age of about 80 percent. The present data showed that considerable inter-year variability may nevertheless occur, and that exceptional climatic events, such as the heavy rainstorm observed during the short rainy season in 1987, may also cause substantial losses in youngstock. Though joining does during the short dry season is likely to produce the largest kid crop, this should nevertheless be avoided since subsequent mortality rates of about 50 percent until the yearling stage represent a serious reduction in biological efficiency. This is because a very large proportion of the resources invested in dams to initiate and maintain pregnancy would be wasted (Lebbie et al., 1996). The existence of a trade-off between maximum reproductive performance and youngstock survival induced by seasonal fluctuations in forage supply should be carefully considered in evaluating management interventions designed to enhance overall goat flock productivity under semi-arid conditions.

3.4.2 Doe survival

As already indicated by the analysis of kid survival, death incidence rates dropped dramatically after one year of age, with mortality rates over the second year of life ranging between 1 and 8 percent. This overall trend was maintained over subsequent life-cycle stages, but patterns in adult female mortality rates differed considerably in shape according to reproductive status, parity, and mating season.

The ranking of mating season groups with respect to survival was similar to that observed in kids, although the differences were much smaller and non-significant. Predicted annual mortality rates ranged between 2.6 and 11.2 percent and were somewhat lower than the 13 percent estimated by Traoré and Wilson (1988) for West African Sahel goats over one year of age in Central Mali. Ba et al. (1996) reported mortality rates over a one year study period in adult West African Djallonké goats of 4.1 percent in vaccinated and dewormed

animals, whereas a rate of 11.5 percent was observed in goats that received a vaccination treatment only. From comparison of these figures to the mortality rate of 16.2 percent observed in the control group, the authors concluded that the deworming treatment was particularly effective in reducing mortality in adult goats. Based on this evidence, it can be concluded that the anthelmintic treatment administered before the rainy seasons in the current experiment may have helped in achieving low levels of mortality, particularly when reproductive stages with high nutrient demands such as late pregnancy and early lactation coincided with periods of increased endoparasitic challenge. Good forage conditions during the latter reproductive stages, coupled with the protective effect of the deworming treatment, thus may explain the exceptionally low level of mortality of 2.6 percent predicted for mating season groups 4 and 5. Inspection of the corresponding hazard curves does not reveal any period of increased susceptibility of breeding females. In contrast, goats giving birth and lactating during the long dry season, as in mating season groups 1 and 2, were exposed to a markedly increased hazard. Typically, no specific cause could be attributed to a large number of the death events, but the majority of goats probably succumbed directly or indirectly to nutritional stress and malnutrition. The hazard curve estimated for mating season group 3 underpins the overriding contribution of plane of nutrition to the risk of death of breeding females. In this group, incidence rates peaked around parturition time, which coincided with the end of the long dry season. Metabolic and nutritional disorders, resulting from an imbalance between nutrient availability and/or intake and nutrient requirements may have been a major source of losses during late pregnancy and the first weeks of lactation. The last weeks before parturition are characterised by an exponential growth in weight of and nutrient requirements for products of conception. Over the same period, however, voluntary intake of energy relative to liveweight of dam is known to decrease (Sauvant et al., 1991), and, during the long dry season, this is further aggravated through an absolute shortage in nutrients supplied from pastures. The discrepancy between energy intake and requirements leads to an increase in lipid mobilization and represents favourable conditions for intense ketogenesis and, consequently, the incidence of pregnancy toxemia. Similarly, negative energy balances and massive losses of body weight due to lipomobilization also occur during the first days of lactation which, coupled with severe energy deprivation, may induce lactation ketosis (Sauvant et al., 1991).

An interesting feature emerging from the analysis was the higher susceptibility of nonpregnant as opposed to pregnant does. Generally, the converse could be expected to be true, since barren does did not endure the increased levels of physiological and nutritional stress associated with gestation and could therefore be assumed to be less sensitive to all kinds of hazards. Certainly, the estimated incidence rates in barren females may have been biased upwards by the small sample size in this category (6 death events out of 21 does at risk). Nevertheless, all events occurred within a few weeks from the onset of mating, thus suggesting that the failure to conceive and subsequent death were causally related.

Mortality rates over the reproductive cycle could be shown to increase linearly with the number of parturitions, and hence age. Corroborative evidence on this finding could not be traced. Compared with the literature on kid mortality under extensive management conditions, there is little information on death rates in adult goats. This is either due to the short duration of many studies, which precludes a full characterization of incidence patterns, or because the focus is exclusively on investigating mortality in youngstock, which is generally regarded to be the primary obstacle to increased productivity in goat herds. However, as has been pointed out by Devendra and Burns (1983), adult mortality plays an important role in determining overall herd productivity. Low mortality rates in breeding females lead to low replacement rates and shift stage abundances in the breeding herd toward higher parities, such that a maximum number of animals will reach the most productive life-cycle stages. Moreover, low replacement rates provide maximum flexibility for actively manipulating herd structure through selective culling of less productive animals. With respect to the present data, the finding that mortality increases with parity, while reproductive performance increases up to the third kidding and declines thereafter, will have consequences for the design of a breeding stock culling policy that it is ment to achieve optimum herd productivity. For instance, from a purely herd dynamics perspective, the inverse relationship between dam survival and reproductive performance with increasing parity can be expected to imply that, conditional upon sufficient availability of replacements, it will generally not be efficient to keep breeding females in the herd beyond their third kidding. Of course, an economic evaluation of the herding enterprise, which would be based on other criteria than maximizing herd growth potential, could well result in more differentiated optimal culling policies for breeding females.

3.4.3 Analytical approach

The following discussion addresses some issues relating to the appropriateness of the type statistical model conventionally used for analysing time-to-event data, as opposed to the logistic regression technique employed in the present work. The ‘classical’ approach (Muenchow, 1986) for analysing survival rates is to subject the proportion or percentage of individuals that died during a fixed observation period to a conventional analysis of variance (ANOVA) or regression analysis, in order to examine the functional

relationship relating this variable to a set of independent variables (or risk factors) that may be either discrete or continuous. The analysis is usually carried out separately for a number of consecutive time end-points within the observation period, so that, implicitly, a cross-sectional perspective is adopted. This type of analysis eventually corresponds to the so-called linear probability model (Agresti, 1990), which appears to be the standard technique employed in livestock-related research. Applications relating to the analysis of mortality in goat flocks can be found in the studies by Gebrelul et al. (1994), Osuagwuh (1991), Traoré and Wilson (1988), Wilson and Light (1986), and Wilson et al. (1985), to cite just a few.

Several problems are associated with the use of the linear probability model. Firstly, ANOVA and regression analysis are intended to be used for analysing means of numeric, normally distributed response measures. Error terms are assumed to be normally distributed with zero mean and a constant variance that is independent of the value of the mean of the response. Clearly, this is not a reasonable assumption for proportions based on binomial responses such as mortality or survival rates. By definition, a dichotomous response variable y_i having possible outcomes 'alive' or 'dead' (coded, for example, as 0 and 1) is distributed as a Bernoulli random variable, whose expected value $E(y_i)$, the probability of dying, determines its variance $var(y_i)=E(y_i)[1-E(y_i)]$. It follows that a model with an additive error component with fixed variance is inappropriate for analysing survival rates, since it cannot accommodate the dependence between mean and variance. The problem becomes particularly acute as $E(y_i)$ moves toward 0 or 1, in which cases the variance moves toward zero. Ordinary least squares estimators are no longer minimum variance in the class of linear unbiased estimators, and their normal sampling distribution does not apply (Agresti, 1990; Neter et al., 1996; Searle et al., 1992). Moreover, given that the response function represents probabilities, the mean responses should be constrained to fall within the interval [0; 1]. Linear response functions do not possess this constraint. Although the problems associated with nonnormal errors terms and nonconstant error variance could be handled by applying a suitable transformation (e.g., the angular transform) to the response values and/or by using weighted least squares estimation, there is no remedy to the structural defect of a linear normal-theory model not to constrain the estimates to fall between 0 and 1 (Agresti, 1990). The ordinary least squares estimator of $E(y_i)$ can result in estimates outside this interval, thus precluding a meaningful interpretation.

The inappropriateness of the linear probability model is easily seen when a closer look is taken at some mortality or survival estimates and their standard errors reported in the literature. As noted above, the linear probability model cannot accommodate the fact that variance moves toward 0 for mortality or survival estimates near 0 or 1. Gebrelul et al. (1994), for example, report percentage mortality rates and standard errors thereof from 15 days to weaning in Alpine, Nubian, and Nubian×Alpine kids of 1.8 (±2), 4.5 (±4), and 5.3 (±3), respectively. Approximate 95 percent large-sample confidence limits for these mean responses are, respectively: [-2.1; 5.7], [-3.3; 12.3], and [-0.6; 11.2]. Clearly, the negative lower interval limits do not allow a meaningful interpretation of these results, and the overestimated standard errors are likely to invalidate all significance tests that are based on the model derived by Gebrelul et al. (1994). A similar problem is apparent with a polynomial regression model reported by Osuagwuh (1991), who studied perinatal reproductive wastage in West African Dwarf goats. The author regressed linear and quadratic dam age on the percentage of neonatal deaths (transformed to the logarithm) in goat kids. Based on the reported regression coefficients and their standard errors, the point estimate of kid mortality for 12 year old dams (33 animals of that age were observed in the sample) can be calculated at 92.7 percent, with approximate 95 percent confidence limits [74.1; 115.8]. Again, the upper confidence limit of more than 100 percent illustrates the kind of spurious results which might be obtained upon fitting linear normal-theory models to mortality data. In light of these difficulties, the latter class of models should not be used for analysing a discrete dependent variable (proportions or rates arising from dichotomous dependent variables). Statistical procedures that explicitly assume binomially distributed errors with an appropriate link function of mean to variance, such as logistic regression, should be preferred instead. Logistic regression, which is a special case of generalized linear models, can be used in situations analogous to the use of regression or analysis of variance or covariance when analysing normally distributed continuous dependent variables (see McCullagh & Nelder, 1983).

A further problem associated with the use of standard ANOVA and regression techniques in analysing time-to-event data is caused by the repeated-observations structure of this type of data. The cross-sectional view adopted by the classical approach ignores the fact that data on the timing of events (e.g., death) are obtained by repeatedly observing individual subjects over time. Survival data, being a special kind of time-to-event data in which the event of interest can only be observed once for each individual under study, are therefore intrinsically longitudinal in nature, and give rise to features which are difficult to handle with conventional statistical methods: censoring, changes in the risk set (i.e., the number of subjects at risk of death at any given point in time), and time dependent covariables. The classical approach is wasteful of information because the event history is totally neglected and, at the same time, it is not clear how it could account for censored or incomplete observations. Possible solutions to the censored data problem consist in omitting all observations that were censored before the time endpoint of interest, or to assigning the maximum length of observation

time as the survival time of all censored cases. However, both approaches have been shown to lead to large biases in estimates of survival rates, while the former approach also leads to an inefficient waste of data (Allison, 1983; Fox, 1993).

In spite of these facts, in livestock-related research most authors do not state whether censoring occurred in their data, and if so, how it was accounted for in their statistical analysis. Censoring is likely to become a major problem particularly in experiments carried out under field conditions. For instance, every animal slaughtered for sale or consumption before the time endpoint of interest would represent a censored observation. A further complication frequently arises due to animals that enter into the herd studied during the observation period. In this case, the population at risk is constantly changing, causing difficulties in estimating the denominator used to calculate mortality or survival rates. Simply averaging the population size measured at various intervals during the study period, as proposed by Putt et al. (1987), does not seem to be a satisfactory solution to this problem. In studying adult mortality in West African Dwarf goat flocks, Ba et al. (1996) used a different method to account for fluctuations in flock size over time. They adjusted data on each animal for the proportion of the observation period that it had spent in the flock by using the total number of animal-days observed on study as denominator. This yields an estimate of incidence rate per day, which can be converted to an annual survival rate by substracting it from 1 and raising the obtained daily survival rate to the power of 365. This method was also recommended by PAN Livestock Services (1991).

Tabelle 1Table 3.8. Effect of different methods of estimation on survival rate estimates. The numerical example was taken from PAN Livestock Services (1991) and shows a population that is censused repeatedly over a one year observation period.

Census date t	Index i	Days since t_{i-1} d_i	Deaths since t_{i-1} s_i	Population size at t_i N_i	Mean pop. size over $[t_{i-1}; t_i]$ $n_i=(N_{i-1}+N_i)/2$	Animal days $A_i=d_i \cdot n_i$	Hazard rate $h_i=s_i/n_i$	Prob. of survival to t_i $p_i=(1-h_i)p_{i-1}$
31.12.89	1			115				1.000
01.03.90	2	59	5	118	116.5	6873.5	0.043	0.957
01.04.90	3	31	24	132	125.0	3875.0	0.192	0.773
01.05.90	4	30	22	129	130.5	3915.0	0.169	0.643
01.07.90	5	61	15	120	124.5	7594.5	0.120	0.565
01.09.90	6	62	5	118	119.0	7378.0	0.042	0.542
01.11.90	7	61	6	125	121.5	7411.5	0.049	0.515
31.12.90	8	61	2	119	122.0	7442.0	0.016	0.507
Total		365	79			44489.5		

	Method of estimating survival rate until end of follow-up			
	1 Life-table estimate: $G_8=\prod_{1\le j<8}(1-h_j)$	2 $1-[\sum_{i=1}^{i=8}s_i/(\sum_{i=1}^{i=8}N_i/8)]$	3 $1-[\sum_{i=1}^{i=8}s_i/[(N_1+N_8)/2]]$	4 $[1-(\sum_{i=1}^{i=8}s_i/\sum_{i=1}^{i=8}A_i)]^{365}$
Estimated survival rate	0.507	0.352	0.547	0.523
Estimated survival rate when N_3=80	0.451	0.316	0.547	0.510

Table 3.8 illustrates the effect of different methods of estimation on survival rate estimates when the risk set changes over time and measurement intervals are of unequal length. In addition to the methods of Putt et al. (1987) and Ba et al. (1996) which were denoted as methods 2 and 4, respectively, a life table estimate (method 1) and an estimate using the average herd size at the start and end of the observation period as denominator (method 3) were also included. Obviously, the choice of method has a dramatic effect on survival rate estimates. Methods 2 and 3 are the ones leading to the largest biases, since changes in the risk set over time are smoothed out (method 2) or not taken into account at all (method 3). A defect common to methods 2, 3 and 4 is to assume a constant force of mortality throughout the observation period, which clearly is not the case, as may be seen from the column reporting hazard rates. This assumption is particularly untenable when there is a strong seasonal variation in risk factors such as nutrient availability or the

prevalence of diseases. The bias introduced by failure to account for nonconstant hazards increases with increasing fluctuations in the risk set and incidence rates over individual time intervals. This effect is shown in Table 3.8 after reducing population size at the third census to 80. While the corresponding increase in the risk of death from 0.192 to 0.242 between third and fourth census is fully reflected in the life-table survival estimate at the end of follow-up, this is only true in part for methods 2 and 4.

In conclusion, if censoring and/or fluctuations in the risk set are present, the life-table estimate is to be preferred over the other estimation methods. Since it is based on hazard estimates for each time interval, both changes in the risk set and censored observations are readily taken into account. The life-table method is particularly well suited for grouped data such as those given in Table 3.8, where event times are not known exactly but are known to have occurred during some interval of follow-up (Allison, 1995). Note that this method of estimating hazard rates is closely related to the logistic regression approach employed in this study. The only difference is that the life-table method is non-parametric, whereas the logistic regression approach used herein models the baseline (logit) hazard function over time parametrically with polynomial splines. This leads to hazard estimates with much smaller variance (Efron, 1988; Gillespie et al., 1994).

The results presented in this study demonstrate the increased structure that can be seen by modelling hazard functions parametrically over time. It provides much more insight into patterns of mortality than the classical method of analysing survival data. Logistic regression is particularly flexible in implementing this approach, and allows comparison among any number of risk groups simultaneously at any time point. As demonstrated in the present study, non-proportionality in death hazard among risk groups can easily be tested or modelled by including interaction terms between time variables and the predictor variables representing these risk groups. Gillespie et al. (1994) and Gray (1992) point out that polynomials or polynomial splines fitted to the logit of the hazard rate form a family of possible distributions which is much richer than the usual parametric alternatives of Weibull, log-normal, log-logistic or gamma. With increasing number of knots, polynomial splines create very flexible families of models that permit explicit estimation of the hazard function rather than treating it as a nuisance parameter like, for instance, in the Cox proportional hazards model. An attractive feature of the logistic regression approach is that it is easily implemented using any standard logistic regression program. Because time (or age, as used in the analysis of youngstock survival) is just another variable in the regression model, the dependence of the hazard on time can take on many different functional forms, which are not limited to polynomials or polynomial splines as used in this study (Allison, 1995). For instance, situations may arise in which a more parsimonious representation may be obtained by letting hazard depend on the logarithm of time.

The possibility of investigating the entire baseline hazard function and its interaction with various risk factors may be considered to be an important advantage over the classical approach of analysing survival data, in which all information of the effect of time on incidence rates is discarded. In livestock-related research this information is of great value, since it allows the identification of critical stages in the production cycle, and provides details on how the associated risks of death differ in magnitude and timing across various risk groups. In general, many factors are involved in a complex way in determining mortality in livestock herds, and it can be expected that a full characterization of patterns of incidence rates will be beneficial in developing management interventions aimed at reducing such mortality.

Chapter 4

Effects of seasonal breeding on productive performance of pastoral goat herds in northern Kenya: a longitudinal analysis of growth in kids and body weight development of does

4.1 Introduction

Goats play an important role in the economy of traditional pastoral production systems in northern Kenya. Goats are kept for both meat and milk production, but overall contribution of goats milk to total milk consumption in pastoral households is limited due to their low milk yields which usually range between 30 and 100 litres per lactation. Hence, the primary output from pastoral goat flocks is meat production both for subsistence consumption and for sale or barter. According to a survey conducted by Schwartz (1986) in Marsabit District, northern Kenya, goat meat can account for more than 70 percent of all meat consumed, and sales of goats and of goat skins can contribute up to about 40 percent of the total annual cash income of pastoral households.

Like other components of performance that determine overall biological productivity of goat herds, such as reproduction and survival, growth and liveweight development in all animal categories are greatly affected by the seasonality in pasture forage production that is typical of semi-arid rangelands in East Africa. The scope for alleviating restrictions imposed on animal performance by the seasonally and annually varying supply of nutrients is very limited. Since pastoral producers lack the ability to manipulate the primary productivity of the grazing system, imbalances between feed supply and nutrient demand from the herd have traditionally been overcome by adaptive management, such as the movement of animals onto pastures with adequate forage production and flexibility in the timing of herd offtake. However, the distinctive advantage derived from herd mobility for compensating nutrient shortages is lost in the transition to sedentariness, an ongoing process which has repeatedly been observed among pastoral communities in semi-arid regions of Kenya (Grandin, 1988, 1991; Fratkin, 1992; Schwartz et al., 1995; Roth, 1996). The reduced mobility of pastoral herds introduces an additional constraint on animal productivity, with repercussions on the welfare of pastoral households.

In this situation, restricting breeding to a short period in a year could help to synchronize seasonal nutrient supply from pastures with the most physiologically demanding stages of the production cycle (Delgadillo & Malpaux, 1996; Walkden-Brown & Restall, 1996). Peak nutrient demand generally occurs from late gestation until weaning, and nutritional deficits during this stage can be expected to lead to low birth weights and milk yields, slow growth, and an increased risk of death of suckling kids. Although local breeds such as the Small East African (SEA) goat have the potential to breed non-seasonally, breeding does may exhibit periods of anovulation or anoestrus as a result of poor feeding conditions. This may be exacerbated if liveweight recovery of dams is inhibited by nutritional stress during the postpartum period, and may cause losses in productivity in subsequent reproductive cycles through lowered fertility, prolificacy, milk production, and survival.

The objective of this study is to investigate whether liveweights and growth performance of youngstock in a herd of SEA goats maintained under pastoral management can be improved by introducing a controlled seasonal breeding regime. Given the importance of liveweight recovery and development of dams for their subsequent reproductive and milk performance, an additional goal is to examine whether, over a reproductive cycle of one year duration, liveweight development of breeding females would benefit from such a change in production strategy.

4.2 Materials and Methods

Experimental data

Data for this study came from a herd of SEA goats maintained at the Ngare Ndare Research Station of the University of Nairobi in Isiolo District, northern Kenya, over a four-year period from 1984 to 1988. The

study area is located 25 km west of the district capital Isiolo at an altitude between 1000 and 1300m. The climate is semi-arid with unreliable rainfall (long-term annual average at Isiolo township: 615 mm) distributed over two wet seasons, the long rainy season extending from March to May and the short rainy season from October to November. The predominant pasture types are annual grassland, dwarf shrub land and Acacia sp. dominated thornbush of medium density. Limited areas of riverine woodlands and perennial grassland on a floodplain serve as dry season grazing reserve.

Details of the experiment with regard to herd management and data recording were described before in Chapters 2 and 3. Briefly, breeding groups of 18 does each, with a balanced age and weight structure, were established. The experiment was initiated at the end of January 1984, when a buck was introduced into the first breeding group for two months. Afterwards, the buck was transferred to consecutive groups for the same duration, so as to achieve year-round mating, kidding, and weaning. Kids were weaned at an age of 16 weeks. For the purpose of analysis, data from the individual breeding groups obtained over the 40 months duration of the experiment were grouped into six different mating seasons. Three complete production cycles, ranging from mating until the time at which youngstock had reached an age of two years were obtained for five of these six consecutive two month mating periods. The sixth period had only two complete cycles, because the last breeding group of the experiment, which was set up by the end of March in 1987, had to be discarded due to incomplete records. The experimental treatment thus consisted of six mating seasons, the first one, labelled as mating season 1, ranged from February to March, and the last one, labelled as mating season 6, ranged from December to January. Mating seasons 4 and 5 (August to October, and October to December, respectively) had to be assumed to have taken place over a period of three months due to a delay of one month which occurred in setting up the first breeding group of mating season 4 in 1984.

Time in the experiment was divided into periods of two weeks, each period starting and ending on a Monday. Routine measurements of weight (kg) of all animals, as well as milk yields of dams were carried out at the beginning of each two-week period. Adult animals were weighed using a weighing crate and measurements were made to the nearest 0.5 kg. Kids were weighed immediately after birth using a spring balance to the nearest 0.25 kg. A total of 8547 measurements were obtained on liveweight and milk production of does; 9837 observations were available on liveweight development of youngstock.

Pasture condition was judged every two weeks using a subjective phenological pasture condition score ranging from 1 to 4 based on greenness and abundance of the herblayer (range condition score [I]), including grasses, herbs, and small dwarf shrubs. Scores of 1 to 2 generally occurred during the dry seasons, and 3 and 4 during and immediately after the rainy seasons. The condition score for the herblayer was upgraded to a maximum score value of 5 to integrate the contribution of bushes and trees with regard to browse availability and the production of high quality litter such as leaves, flowers and fruits (range condition score [II]).

Traits studied

Growth rates of kids, expressed as average relative daily liveweight gains ($g \cdot kg^{-0.75} \cdot day^{-1}$) were analysed from birth until two years of age at 4 weeks intervals. Relative live weight gain was calculated as the difference between two consecutive live weight measurements divided by the length of each time interval (28 days) and the average of the two live weight measurements raised to the power of 0.75. Animals with complete records over the follow-up period of 104 weeks thus had 27 observations. In order to reduce both execution times of model estimations and the complexity of growth curves fitted to the data, separate analyses were carried for the time series from birth until 50 weeks, and from 52 until 104 weeks of age.

Average absolute daily live weight gains ($g \cdot day^{-1}$) over time intervals of 16 weeks each were studied from birth until 96 weeks of age (resulting in 6 observation times for subjects with complete records). These were computed as the difference between two consecutive live weight measurements, 16 weeks apart, divided by the length of the time interval (128 days). Liveweight development of kids (kg) was studied at 8 week intervals, ranging from birth until two years of age. Hence, subjects with complete records had 14 observation times. For all the foregoing traits, observations for immature females which were first mated before reaching the age of 104 weeks were considered to be censored observations from the time at mating onwards, and the corresponding records were deleted from the data set.

Body weight (kg) development of does during pregnancy was studied at biweekly intervals over a period of 52 weeks, such that subjects with complete records had a maximum of 27 observation time points in the analysis. Only those animals with live-birth events were considered. A time series was constructed from the body weight measurements of each doe, ranging from the recording date at the onset of mating to the recording date 52 weeks later. Whenever does were rebred or were found to be pregnant before the end of the current reproductive cycle, observations from this time point onwards were considered to be censored and deleted from the data set. In order to study relative live weight changes over the reproductive cycle, the same

series of measurements was used to compute percentage change in live weight at each time point, relative to body weight observed at mating.

Statistical analysis

In studying patterns of growth and liveweight development, liveweight is a variable measured repeatedly over time in the experimental units. Principally, this type of sequential, correlated observations can be analysed with multivariate regression techniques. However, longitudinal studies typically give rise to special data structures which do not meet model assumptions imposed by such methods (Verbeke, 1997). A very often encountered problem in the analysis of growth data is that individual animals may be observed a different number of times because they were withdrawn from the experiment for some reason or died prior to the final measurement time. Moreover, time points at which repeated measurements are taken may not be the same for all subjects on study, and the intervals between observations may be different as well. An alternative to multivariate regression which is able to accommodate incomplete and unequally spaced observations is the linear mixed-effects model (Laird & Ware, 1982; Cnaan et al., 1997). This approach is also well-suited for modelling covariances among observations on the same subject and for handling heterogeneous variances over time (Wolfinger, 1996).

The general linear mixed model framework, as implemented in the SAS procedure MIXED (SAS Release 6.12, 1996), was used to fit growth curve models to longitudinal growth and liveweight development data. The aim was to characterize patterns of growth and liveweight change over time for subjects in the six different mating season groups, and to investigate the effects of other covariates on these patterns. The basic premise in growth curve models is that there is a functional relationship between the observed response, a treatment effect, and time. One possible way of approximating the actual functional form of the relationship is through a natural polynomial or polynomial splines in time (Rowell & Walters, 1976; Smith, 1979; Cullis & McGilchrist, 1990), and this approach was adopted in the present study.

Two sources of variation that are potentially present in longitudinal data can be distinguished. First, there is subject to subject variation in the mean response value which can be taken into account by including a random subject factor into the model. It is this between-subject random effect which causes the correlation within each subject's observations. The second random component is the within subject error. This random effect consists of measurement errors and the actual variability of the individual subject's response (Jones, 1993). Typically, whenever a response variable is measured repeatedly over time, there is the possibility of serial correlation. Serial correlation is present when measurements within a subject taken close in time are more highly correlated than measurements taken far apart in time. However, Diggle et al. (1995) point out that, although serial correlation would appear to be a natural feature in any longitudinal data model, in many applications its effects may be dominated by the combination of random subject effects and measurement errors. A general description of the models used for analysing longitudinal data is given below.

Measurements (absolute and relative growth rates and liveweight changes calculated from liveweight measurements, as well as liveweight measurements themselves) were obtained from the same unit of observation (individual kids or does), i , i=1,..., n, in the jth treatment group, j=1,..., q, at p pre-specified time points, and subjects were assigned randomly to one of the q treatment groups. Then, following Laird and Ware (1982), the general linear mixed model for a sequence of p measurements on subject i is

$$y_i = \mathbf{X}_i\beta + \mathbf{Z}_i\gamma_i + \varepsilon_i, \qquad (1)$$

where

y_i = a $p_i \times 1$ vector of the response variable for subject i
$\mathbf{X}_i$ = a known $p_i \times q$ design matrix
β = an unknown $q \times 1$ vector of fixed effects coefficients
$\mathbf{Z}_i$ = a known $p_i \times r$ design matrix
γ_i = an unknown $r \times 1$ vector of random subject coefficients, assumed to be independently distributed across subjects with distribution $\gamma_i \sim N(0, \sigma^2\mathbf{B})$, where $\mathbf{B}$ is the between subjects covariance matrix
ε_i = a $p_i \times 1$ vector of within subjects errors assumed to be distributed as $\varepsilon_i \sim N(0, \sigma^2\mathbf{W}_i)$, where $\mathbf{W}_i$ is the within subjects covariance matrix

The columns of the model matrices $\mathbf{X}_i$ and $\mathbf{Z}_i$ consist of indicator variables corresponding to the levels of the fixed and random subject effects, respectively. The between individuals design matrix $\mathbf{X}_i$ can specify polynomial powers of the times of observation, treatment and/or classification factor effects and their

interactions with polynomial terms, as well as time-changing covariates such as the range condition scores in the present study (Jones, 1993; Cnaan et al., 1996).

The general linear mixed model (10) extends the general linear model by allowing a more general specification of the covariance matrix of ε_i. It allows for both correlation and non-identicalness, although normality is still assumed. The second difference lies in the addition of the known design matrix, $\mathbf{Z}_i$, and the vector of unknown random subject effects, γ_i. These between subject components of variance can be used to model the random deviations of the intercept and possibly higher degree polynomial trends in time for subject *i* from the subject's group mean intercept and higher degree polynomial powers of the times of observation. The linear mixed model formulation is very general since different subjects can have different numbers of observations as well as different numbers of observation times. Therefore, subjects with incomplete data do not need to be discarded from the analysis (Cnaan et al., 1996). Equation (1) can further be expanded to incorporate additional random effects by defining a $p_i \times v$ design matrix, $\mathbf{U}_i$, of random effects and a corresponding unknown $v \times 1$ vector, τ_i, of random effects coefficient s_i. The random effects, $\square_i$, are assumed to be identically and independently distributed as $\tau_i \sim N(0, \sigma^2\mathbf{I})$, where $\mathbf{I}$ denotes the $p \times p$ identity matrix. In the present study, the effect of production cycle (three levels) and its interaction with the mating season treatment were considered as such random effects and included in all initial models fitted to the data.

Model construction and data analysis encompassed several steps. As a starting point, for each response variable individual profiles and group mean curves were plotted to obtain a visual picture of possible models for the data, including an appropriate variance-covariance structure for the within-subject errors. Based on this preliminary inspection, various models that included random subject effects and serial correlation were computed. Since serial correlation can partially be confounded with the random between subject effects, the procedure recommended by Jones (1993) was used to find an adequate model. It involves fitting four different models, one with uncorrelated (compound symmetry) error structure, one with random subject effects alone, one with a serially correlated within subject error structure alone, and one with both random subject effects and serially correlated error structure. Two additional models, one with and one without random subject effects were fitted to the data using the most general form of heterogeneous variances and covariances, that is, an unstructured covariance matrix. Akaike's Information Criterion (AIC) was then used to select the best fitting model. The serial correlation structure used was a heterogeneous first-order autoregressive structure (ARH[1] in the SAS PROC MIXED terminology). PROC MIXED uses the parameterisation illustrated by the following 3×3 matrix:

$$\begin{bmatrix} \sigma_1^2 & \sigma_1\sigma_2\rho & \sigma_1\sigma_3\rho^2 \\ \sigma_2\sigma_1\rho & \sigma_2^2 & \sigma_2\sigma_3\rho \\ \sigma_3\sigma_1\rho^2 & \sigma_3\sigma_2\rho & \sigma_3^2 \end{bmatrix}$$

Here, σ^2_1, σ^2_2, and σ^2_3 are the variance parameters at each of three consecutive measurement times, and ρ is the autoregressive parameter. Thus, with the ARH[1] covariance structure a different variance is estimated for each measurement time, such that variance heterogeneity over time can be accounted for in the analysis.

Table 4.1 summarizes the predictor variables included in preliminary analyses of longitudinal data. Selection of suitable final models was based upon fitting successive nested model versions, and omitting variables from the linear predictor when the likelihood ratio (LR) statistic indicated that the model including an additional parameter did not fit significantly better than the simpler model. Fixed-effects terms and interactions among fixed-effects were excluded from the model when the probability of obtaining a greater χ^2-value than the observed LR test statistic from a χ^2 distribution with *r* degrees of freedom was greater than 0.15, *r* denoting the additional parameters that have to be estimated in the larger of the two models. The same procedure was applied to test for the significance of random effects, except that the *p*-value for the LR statistic was obtained by taking half of the probability of a greater χ^2 from a χ^2 distribution with one degree of freedom, given that only a one-sided test is needed in this case and only one additional parameter is estimated upon including a random effect into the model.

When fitting polynomial growth curves, multicollinearity between different polynomial degrees of a quantitative predictor variable can occur and cause computational as well as interpretational difficulties (Steel and Torrie, 1980). Since the polynomial representation of response over time used in the present context resulted in high pairwise correlations between powers of time, a matrix of orthogonal polynomials in time was constructed following the procedure described in Draper and Smith (1981) and used in fitting response curves. In order to control the experimentwise error rate at the prespecified level of α=0.05 when making multiple comparisons of factor level means, both the Bonferroni and Tukey multiple comparison procedures were used. The procedure giving the narrower confidence limits was then chosen to report

significance probabilities of differences in factor level means. This choice is proper since it does not depend on the observed data (Neter et al., 1996). Tests of hypotheses concerning specific linear combinations of parameter estimates were obtained by specifying appropriate *estimate* and *contrast* statements in the MIXED procedure.

Table 4.1. Explanatory variables included in initial models fitted to longitudinal data. For random effects, nesting factors are given in square brackets. (PC=production cycle; MS=mating season; RC=range condition).

Outcome	Random effects	Fixed effects
Liveweight (kg) and relative liveweight change (%) in does over a reproductive cycle of one year duration	• dam[PC×MS] • production cycle (1; 2; 3)	• mating season (1 to 6) • parity at breeding (0; 1; 2; ≥3) • weight at breeding in kg (<25; 25 to 30; 30 to 35; 35 to 40; ≥40) • type of birth (single; twins) • Lagged median range condition score[I] and [II] for the current and the two immediately preceding periods (integer scores of 1 to 4, and 1 to 5, respectively) • time
Liveweight (kg) of kids from birth to 104 weeks of age over a reproductive cycle of one year duration	• kid • dam[PC×MS] • production cycle	• mating season • dam parity at breeding (0;1;2;3; ≥4) • dam weight postpartum in kg (<30; 30 to 35; 35 to 40; ≥40) • milk yield until weaning in kg (<22.5; 22.5to32.5;32.5to42.5;42.5to52.5; ≥52.5) • litter size • sex • time
Growth of kids ($g \cdot kg^{-0.75} \cdot day^{-1}$) from birth until 50 weeks, and from 52 until 104 weeks of age	• kid • dam[PC×MS] • production cycle	• mating season • dam parity at breeding • dam weight postpartum in kg • milk yield until weaning in kg • litter size • sex • lagged median RC scores I+II at each time point • time
Mean absolute weight gains ($g \cdot day^{-1}$) of kids from birth to 96 weeks	• kid • production cycle	• mating season • sex • time

4.3 Results

4.3.1 Growth performance of kids

Daily weight gains

The analysis of growth rate in kids in terms of relative ($g \cdot kg^{-0.75} \cdot day^{-1}$) and absolute ($g \cdot day^{-1}$) daily weight gains revealed neither a significant component of variance due to dam [mating season×production cycle], nor significant individual differences (random kid effect). Also, both maternal parity stage and postpartum weight had no influence on response patterns. Interestingly, differences in relative body weight gains between female and male kids were very small and insignificant in all the analyses performed on this trait. In contrast, *absolute* daily growth rates differed markedly between male and female offspring.

Table 4.2. Tests of fixed effects and estimates of variance components and covariance parameters for growth curve models fitted to daily weight gains of kids ($g \times kg^{-0.75} \times day^{-1}$), accounting for the effects of mating season.

birth to 50 weeks of age				*52 to 104 weeks of age*			
Fixed effects	*df*	χ^2	$p>\chi^2$	*Fixed effects*	*df*	χ^2	$p>\chi^2$
Mating season	5	2.7	0.746	Mating season	5	6.9	0.227
t	1	1291.0	<0.001	t	1	20.0	<0.001
t^2	1	654.2	<0.001	t^2	1	0.1	0.950
t^3	1	342.3	<0.001	t^3	1	0.1	0.759
t^4	1	190.8	<0.001	t^4	1	1.7	0.190
t^5	1	39.4	<0.001	t^5	1	0.3	0.578
t×matingseason	5	25.1	<0.001	t^2×matingseason	5	55.7	<0.001
t^2×matingseason	5	48.3	<0.001	t^3×matingseason	5	13.4	0.020
t^3×matingseason	5	24.2	<0.001	t^4×matingseason	5	65.5	<0.001
t^4×matingseason	5	52.4	<0.001	t^5×matingseason	5	27.9	<0.001
t^5×matingseason	5	15.1	0.010				

Within-subject Covariance parameters *)	*age interval* [*weeks*]	*estimate*	*std. error*	*Within-subject Covariance parameters* *)	*age interval* [*weeks*]	*estimate*	*std. error*
σ^2	0-2	552.2	45.1	ρ		-0.12	0.03
	4-6	220.9	18.3	σ^2	50-52	116.9	11.6
	8-10	126.9	10.7		54-56	99.1	10.1
	12-14	129.9	11.3		58-60	112.3	11.9
	16-18	160.0	14.1		62-64	123.6	13.6
	20-22	155.9	14.0		66-68	141.9	16.1
	24-26	94.2	8.5		70-72	107.4	13.1
	28-30	94.1	8.6		74-76	141.9	18.1
	32-34	137.1	12.8		78-80	130.7	18.2
	36-38	112.0	10.6		82-84	67.7	9.8
	40-42	103.0	9.9		84-86	116.7	17.9
	44-46	110.5	10.7		88-90	98.3	16.7
	48-50	89.8	8.9		92-96	132.6	24.7
					98-100	89.0	17.4
					102-104	67.3	13.7

Variance components			*Variance components*		
σ^2PC	2.80	2.28	σ^2PC×MS	1.40	0.70
σ^2PC×MS	1.65	0.77			

*) ρ=autoregressive parameter standing for the correlation between adjacent observations on the same subject; σ^2=variance of an observation in a given age interval; MS=mating season; PC=production cycle. Note that standard errors for variance components are based on asymptotic normality.

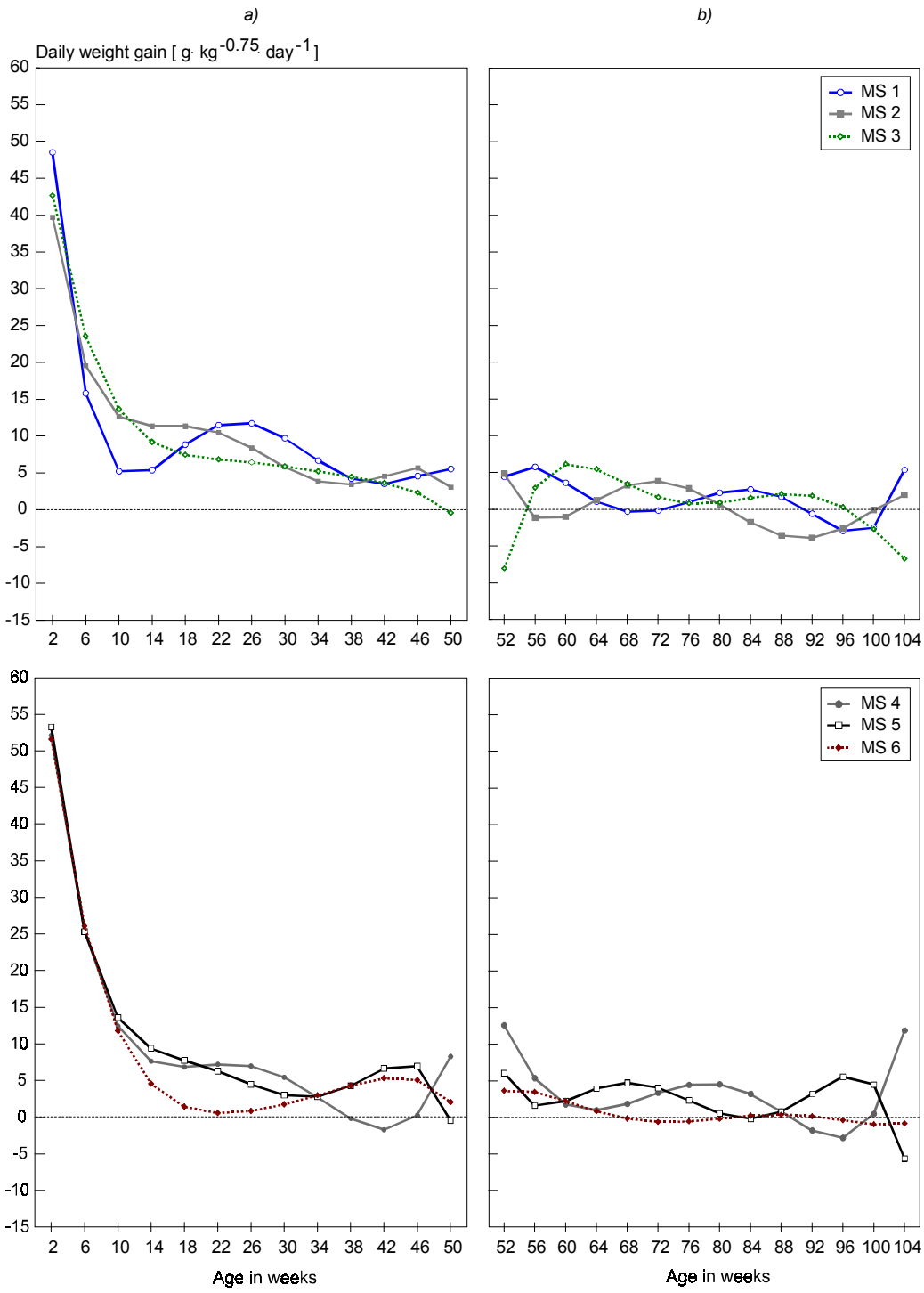

Figure 4.1. Estimated relationships (least-squares means) between daily weight gains by mating season (MS) and age of kids from *a)* birth until one year of age, and *b)* from one to two years of age.

Relative daily weight gain data were modelled as a polynomial function in time differing according to *a)* mating season, and *b)* litter size, milk yield until weaning, and lagged range condition scores [I] and [II] (Tables 4.2 and 4.3). The decision to fit separate models in assessing the latter effects was motivated by the fact that they are nonmanipulable or observational classification factors, and that they had been found to be influenced by, or confounded with, the control variable determining functional relationships in this study, i.e. mating season. Models developed to assess the effects of litter size, milk yield until weaning, and lagged range condition scores [I] and [II] were restricted to the period from birth until the yearling stage. This was done primarily because the assessment of range condition was discontinued in November 1987 before surviving kids born in early 1986 and thereafter had reached an age of two years. Additionally, litter size and milk yield until weaning did not significantly affect relative daily weight gain beyond one year of age.

Table 4.3. Tests of fixed effects and estimates of variance components and covariance parameters for growth curve models fitted to daily weight gains of kids ($g \times kg^{-0.75} \times day^{-1}$) until 50 weeks of age, accounting for the effects of milk yield until weaning, litter size, and ***a)*** lagged median range condition score [I] and ***b)*** lagged median range condition score [II].

	a)				***b)***		
*Fixed effects**)*	*df*	χ^2	$p>\chi^2$	*Fixed effects**)*	*df*	χ^2	$p>\chi^2$
MILK16	4	19.7	<0.001	MILK16	4	21.0	<0.001
Litter size	1	0.7	0.415	Litter size	1	0.6	0.437
RC [I]	3	80.8	<0.001	RC [II]	4	271.1	<0.001
t	1	1305.2	<0.001	t	1	1238.9	<0.001
t^2	1	640.8	<0.001	t^2	1	642.4	<0.001
t^3	1	358.5	<0.001	t^3	1	383.6	<0.001
t^4	1	183.5	<0.001	t^4	1	190.0	<0.001
t^5	1	35.4	<0.001	t^5	1	36.4	<0.001
t×MILK16	4	17.0	0.002	t×MILK16	4	22.3	<0.001
t^2×MILK16	4	19.8	0.001	t^2×MILK16	4	17.6	0.001
t^3×MILK16	4	8.6	0.071	t^3×MILK16	4	8.8	0.068
t×litter size	1	9.0	0.003	t×litter size	1	11.7	0.001
t^2×litter size	1	5.5	0.020	t^2×litter size	1	6.0	0.014
t×RC [I]	3	31.7	<0.001	t×RC [II]	4	49.9	<0.001
t^2×RC [I]	3	8.0	0.046	t^2×RC [II]	4	15.8	0.003
t^3×RC [I]	3	8.2	0.042	t^3×RC [II]	4	13.2	0.010
*Within-subject Covariance parameters***)*	*age interval [weeks]*	*estimate*	*std. error*	*Within-subject Covariance parameters***)*	*age interval [weeks]*	*estimate*	*std. error*
σ^2	0-2	544.6	44.4	σ^2	0-2	516.6	42.0
	4-6	213.0	17.6		4-6	226.1	18.7
	8-10	131.8	11.1		8-10	129.4	10.9
	12-14	130.6	11.3		12-14	129.0	11.1
	16-18	161.5	14.2		16-18	158.1	13.9
	20-22	160.0	14.3		20-22	149.4	13.4
	24-26	107.2	9.6		24-26	103.4	9.3
	28-30	98.9	9.0		28-30	92.5	8.4
	32-34	131.1	12.2		32-34	124.6	11.6
	36-38	109.0	10.3		36-38	106.4	10.0
	40-42	110.9	10.9		40-42	108.1	10.6
	44-46	119.7	12.0		44-46	114.5	11.4
	48-50	80.2	8.2		48-50	83.2	8.5
Variance components				*Variance components*			
σ^2_{PC}		4.14	3.02	σ^2_{PC}		4.34	3.15

*) MILK16=milk yield until weaning; RC[I], RC[II]=lagged median range condition scores [I] and [II] in each age interval.

**) σ^2=variance of an observation in a given age interval; PC=production cycle. Note that standard errors for variance components are based on asymptotic normality.

Estimates of absolute growth rate were obtained by fitting an additional model to average body weight gains from birth to 96 weeks for a total of six consecutive life stages, each of 16 weeks duration. Here, only mating season and sex of kid systematically affected observed outcomes (Table 4.4).

Estimated relationships between kid age and relative daily weight gains by mating season are depicted in Figure 4.1. A fifth order polynomial in time was necessary in order to adequately represent relative weight

gains until one and two years of age (Table 4.2). The highly significant interactions of mating season with the various polynomial time trends resulted in completely different response curves for each for each of the six mating season groups. A notable feature of the analysis from birth to one year of age is that no serial correlation between adjacent observations on the same subject was present in the data. The covariance structure used was therefore an unstructured matrix, with zero covariance among subsequent measurements, but heterogeneous variances across time. Although very small in magnitude (ρ=-0.12), correlated within-subject errors occurred from year one onwards, and a heterogeneous first-order autoregressive structure was found to be the most appropriate structure for modelling relative weight gains up to two years of age. Thus, during the period from birth until 52 weeks, intensities of growth were serially independent across age intervals and appeared to be determined mainly by environmental conditions, as is illustrated by the large and recurrent fluctuations in responses over time (Figure 4.1). Beyond 52 weeks of age, the small negative first-order autoregressive coefficient lead to an alternating pattern of autocorrelations, reflecting a tendency for responses to oscillate about a slightly positive mean relative growth. However, the correlation between observations separated by two time steps is almost nil ($(-0.12)^2 = 0.014$), indicating a weak dependence of current on past growth performance. The covariance parameter estimates for both models in Table 4.2 clearly illustrate the variance heterogeneity in relative liveweight gain over time, and underline the importance of using a heterogeneous covariance matrix in modelling within-subject errors. Finally, there was a small, but highly significant variation attributable to the effect of production cycle, and to its interaction with mating season ($p < 0.01$).

Generally, it should be emphasized that the number of animals for which there were performance records diminished considerably in age intervals beyond 70 weeks of age, either because animals were taken off for slaughter or, in the case of replacement females, because they were transferred into the breeding herd. Daily weight gain estimates over this time period were therefore less reliable than those for age intervals between birth and one year of age. This is particularly true for estimates relating to mating season 6, for which no data had been obtained during the first production cycle.

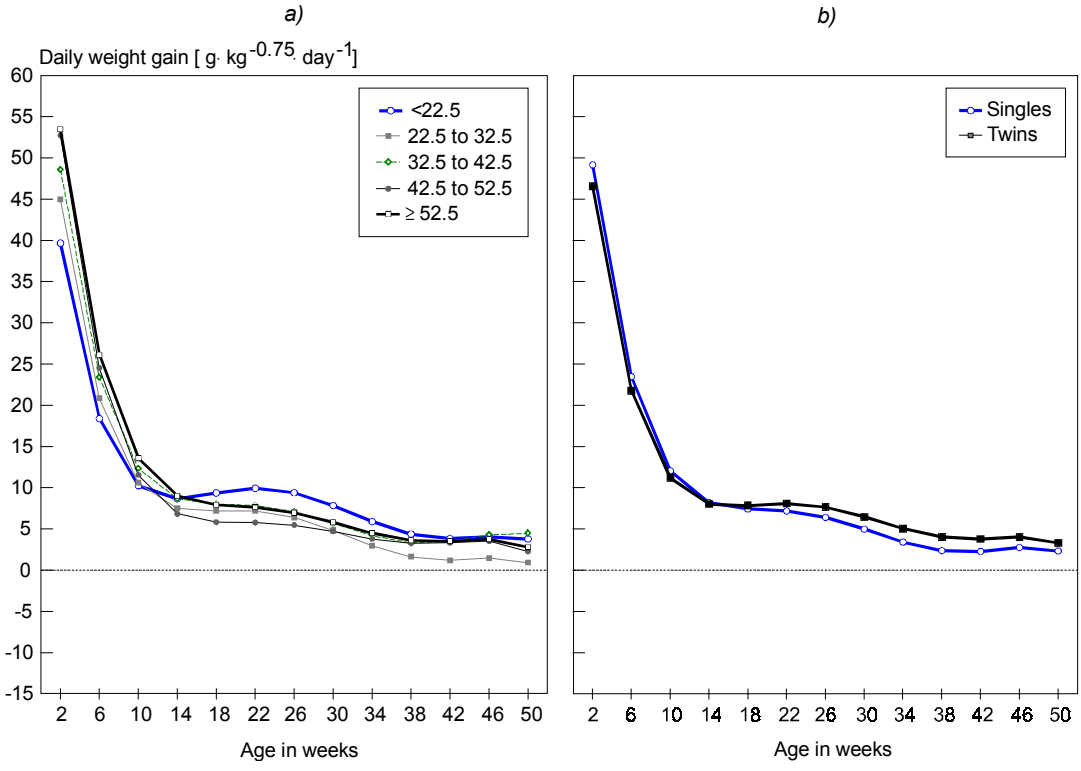

Figure 4.2. Relationships (least-squares means) between daily weight gains and age of kids, according to *a)* milk yield until weaning and *b)* litter size (estimates were obtained from model a) in Table 4.3).

Kids born in mating season group 5 displayed the highest initial propensity to growth (0 to 4 weeks), with an estimated growth rate of 53 $g \cdot kg^{-0.75} \cdot day^{-1}$, closely followed by kids in groups 4 and 6 (both $52 g \cdot kg^{-0.75} \cdot day^{-1}$). In these three groups, births took place between the months of December and May, during which, in general, favourable pasture conditions prevailed. In contrast, kids born during the long dry season

(group 2) grew at a significantly lower rate of 40g·kg$^{-0.75}$·day^{-1} ($p< 0.05$) during the first four weeks of life. Intermediate weight gain levels of 48 and 43g·kg$^{-0.75}$·day^{-1} during the same age interval were estimated for mating season groups 1 and 3, respectively.

The fastest decline in growth rate after 4 weeks of age occurred in group 1, in response to declining milk yields as the long dry season progressed. Within ten weeks from birth, growth slowed down to a rate of 5 g·kg$^{-0.75}$·day^{-1}, which corresponded to only 41 percent of the mean weight gain achieved by kids in all other groups in the age interval of 8 to 10 weeks ($p< 0.01$). As expected, the rate of decline in relative growth was less pronounced when kids were born during the short rains (group 3) and just prior to (group 4) or during the long rainy season (group 5). In the latter treatment groups, nutritional constraints did not seem to significantly lower early growth in kids, since daily weight gain in kids remained well above 5g·kg$^{-0.75}$·day^{-1} until at least 24 weeks of age. Despite their low initial intensity of growth, offspring born in mating season group 2 displayed comparatively high growth rates of about 13 (8-10 weeks) to 10 g·kg$^{-0.75}$·day^{-1} (20-22 weeks) after the sixth week. In this group, kids probably benefited both from increased levels of available nutrients as forage growth and quality improved at the start of the short rainy season, and from concurrent increases in milk yields of does.

Kids in mating season group 1 showed a remarkable recuperative capacity around the time of weaning, when quantity and quality of forage on offer began to improve at the onset of the short rains. Relative growth rates more than doubled between 14 and 20 weeks of age and reached a maximum value of 12 g·kg$^{-0.75}$·day^{-1} at 24 to 26 weeks. Under the same environmental conditions, compensatory gains achieved in group 6, after the retardation in growth experienced during the long dry season between 16 and 28 weeks of age, were much less pronounced and levelled-off at approximately 5 g·kg$^{-0.75}$·day^{-1}. With a displacement in time of two months, the estimated relative weight gain curve for mating season group 5 followed a similar pattern. Except for the peaks in growth rate at about one and two years of age (8 and 12 g·kg$^{-0.75}$·day^{-1}, respectively) observed in group 4, the response profiles in Figure 4.1 generally indicate that the rate and persistency of compensatory gains after periods of nutritional stress tended to decline with advancing age. However, even at late stages (>52 weeks) were kids observed to be able to more than offset delays in growth as well as weight losses by considerably increasing growth intensity during the rainy seasons, where maximum relative liveweight gains of about 5 g·kg$^{-0.75}$·day^{-1} were attained. Responses in mating season group 6 differed noticeably from this overall pattern, in that liveweight development slowed down rapidly beyond one year of age, and the capacity to fully compensate past poor growth performance was virtually absent. In this group, nutritional constraints experienced at early developmental stages (16 to 30 weeks) seemed to have caused permanent stunting from about 64 weeks onwards.

Models fitted to evaluate growth performance in terms of litter size, milk yield until weaning, and range condition scores are presented in Table 4.3. Trends across time in factor level means for all variables considered differed noticeably, as may be seen from the significant interactions of litter size, milk yield until weaning, and range condition scores with polynomial time terms and from the estimated response profiles displayed in Figures 4.2 and 4.3. Likewise to the model fitted to relative weight gains until 52 weeks that contained mating season as the sole explanatory variable, no serial correlation between adjacent measurements on the same subject could be detected, but again, variances were found to be heterogeneous across time. Variation among production cycles was small, but highly significant ($p< 0.01$), and therefore was included in the final models.

Clear superiority in growth until 10 weeks of age was shown by kids which had least restrictions in terms of milk availability (≥52.5 kg), with relative weight gains that declined from initially 54 g·kg$^{-0.75}$·day^{-1} to 14 g·kg$^{-0.75}$·day^{-1} at 8 to 10 weeks of age (Figure 4.2). Growth intensity was much lower ($p< 0.05$) in kids born to does producing less than 22.5 kg milk until weaning, with estimated rates of gain of 40 g·kg$^{-0.75}$·day^{-1} within the first two weeks of life, and 10g·kg$^{-0.75}$·day^{-1} in the 8 to 10 weeks age interval. Until 10 weeks of age, a significant linear trend ($p< 0.01$) in relative growth rates across milk yield levels was observed.

An interesting feature emerged as kids approached the weaning stage. Kids which had access to very low quantities of milk during the suckling period (< 22.5 kg) showed an increasing intensity of growth from 14 weeks onwards, reaching a maximum of 10 g·kg$^{-0.75}$·day^{-1} at 20 to 22 weeks of age, well above that achieved in all other milk yield classes in which growth slowed down steadily with advancing age. Offspring in the former milk yield class were able to maintain the highest growth intensity until at least 34 weeks. As is evident from the response profiles depicted in Figure 4.2, the linear trend in relative weight gains across milk yield levels disappeared beyond about 10 weeks of age, which indicates that body weight development in kids became increasingly independent of the amount of milk produced by their dams. This is particularly true for kids which received very low milk quantities, such that they probably had been effectively weaned at an earlier stage.

Single born kids grew more intensively than twin born kids before 10 weeks of age, although this difference was statistically significant ($p< 0.05$) only within the first four weeks of life. From 20 weeks onwards, this trend was reversed and relative growth rates of twins exceeded those of singles by 13 (20-22 weeks; $p< 0.05$) to as much as 68 percent (36-38 weeks; $p< 0.05$). By 42 weeks of age, differences in rates of weight gain due to litter size were no longer significant.

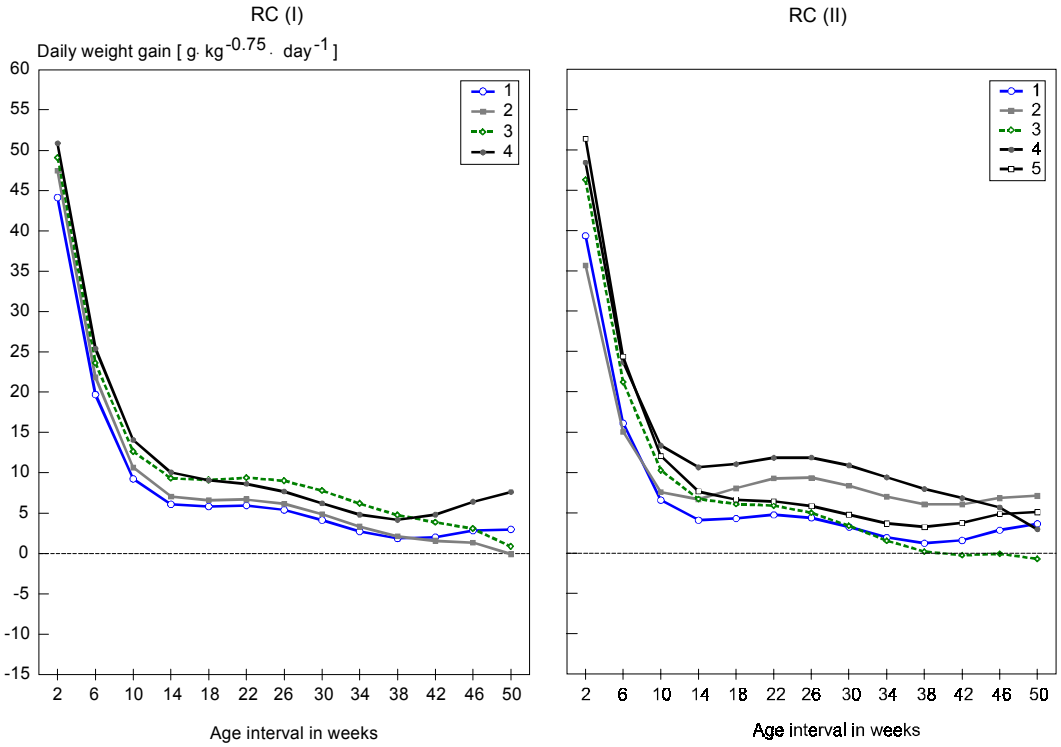

Figure 4.3. Effect of lagged median range condition scores on daily weight gains of kids until 50 weeks of age.

Pasture condition, as measured by the two range condition scores, had a considerable effect on relative growth performance of kids (Figure 4.3). Differential effects of RC score [I] levels were generally less pronounced than those of RC score [II]. Until 14 (RC [I]) and 10 weeks of age (RC [II]), relative weight gains followed the expected pattern and were found to be an increasing function of range condition in each age interval. During the suckling period, this relationship was certainly mediated through the effect of pasture quality on milk production. For lagged RC score [I], significant differences were found between levels 1 and 4 at all ages, between levels 1 and 3 from 20 to 38 weeks, and between levels 2 and 3 from 12 to 38 weeks ($p< 0.05$). Response patterns for levels 1 and 4 became inconsistent beyond 38 weeks of age. This was mainly due to the influence exerted by extreme values in weight gains, observed in both of these levels at the end of the time frame, on the estimation of the respective response curves. These would have been smoothed out upon including later age intervals into the analysis.

Several inconsistencies occurred with respect to estimated effects of lagged RC [II] scores on relative weight gains beyond 10 weeks of age. Firstly, estimates for score level 2 in each age interval considered were based on few observations ($N< 10$) and, therefore, were probably seriously biased. This might account for the fact that in this case relative growth rates were predicted to increase, after 14 weeks of age, above those achieved at score values of 1, 3, and 5. Secondly, the sharp decline in response for level 5 from 8 weeks onwards was unexpected, and no clear-cut explanation for this pattern could be identified. The same was true for the estimated trend in weight gains for the third level after 30 weeks of age. Nevertheless, until 42 weeks, relative growth was significantly lower under very poor pasture conditions (level 1) than under favourable conditions (level 4, $p< 0.01$). From 8 to 44 weeks, lagged RC [II] score values of 3 and 5 also led to slower weight gains than score values of 4 *(*$p< 0.05$).

A summary of the model fitted to evaluate absolute daily weight gains in terms of mating season and sex of kid is given Table 4.4. The estimated covariance parameters show that average daily weight gains achieved in consecutive age intervals were only weakly correlated (ρ=-0.21). Two important features emerged from the

Table 4.4. Tests of fixed effects and estimates of variance components and covariance parameters for the model fitted to daily weight gains of kids (g×day^{-1}), accounting for the effects of mating season and sex.

Fixed effects	*df*	χ^2	$p>\chi^2$	*Within-subjects covariance parameters**)	*age interval* [*weeks*]	*estimate*	*std. error*
Mating season	5	2.6	0.760	ρ		-0.21	0.03
Sex	1	10.4	0.001	σ^2	0-16	488.9	42.2
t	1	878.5	<0.001		16-32	227.8	21.0
t^2	1	124.7	<0.001		32-48	195.2	19.1
t^3	1	64.7	<0.001		48-64	306.7	33.4
t^4	1	1.4	0.246		64-80	413.9	56.0
t^5	1	1.4	0.239		80-96	521.5	93.8
t×matingseason	5	27.8	<0.001				
t^2×matingseason	5	39.6	<0.001	*Variance components*			
t^3×matingseason	5	113.5	<0.001				
t^4×matingseason	5	138.4	<0.001	σ^2_{PC}		122.1	88.2
t^5×matingseason	5	159.1	<0.001	$\sigma^2_{PC\times MS}$		11.0	4.7
t×sex	1	7.9	0.005				
t^2×sex	1	11.3	0.001				

*) ρ=autoregressive parameter standing for the correlation between adjacent observations on the same subject; σ^2=variance of an observation in a given age interval; MS=mating season; PC=production cycle. Note that standard errors for variance components are based on asymptotic normality.

analysis of absolute weight gains in comparison to the results reported previously for relative growth rates in kids. Firstly, the fact that sex of kid significantly affected average daily weight gains in absolute, but not in relative terms, shows that the faster growth rate observed in males is probably entirely due to their higher initial liveweight state, and not to a higher intrinsic propensity for growth. Secondly, a much larger part of the variation observed in responses was attributable to the effect of production cycle, and to its interaction with the mating season treatment effect, than was the case for relative weight gains. The latter variance components cause a vertical shift in BLU-predicted response profiles (i.e., in the intercepts), but do not affect the shape of factor level trends over time. And if it is true that, *ceteris paribus*, absolute growth rates are primarily a function of liveweight state, then these variations could, to a large extent, be explained by differences in birth weight between replications of the experiment.

Table 4.5 provides estimates of average weight gains by mating season group and sex. Average preweaning gains of about 83 g·day^{-1} were achieved when suckling took place between end of October and end of June (groups 3, 4, and 5), and diminished considerably with further displacement of the weaning stage into the long dry season (groups 6 and 1). Compared to offspring in the former groups, suckling kids in group 1 gained weight at a significantly lower rate of 59 g·day^{-1}, but were able to compensate for their poor preweaning performance by maintaining growth at similar levels during the following eight months of life. Almost identical average daily postweaning gains were achieved by kids born in mating season group 2. Over the same development stage, decreasing pasture quality in the long dry season caused a significant retardation in growth in groups 5 and 6. However, net average weight losses only occurred during the second year of life in mating season group 2 (48-64 and 80-96 weeks), 4 (80-96 weeks), and 6 (64-80 weeks). In all three cases, these weight losses were associated with nutritional stress experienced during the dry seasons.

Table 4.5. Least-squares means and standard errors (in parentheses) of body weight gains ($g \times day^{-1}$) in kids over six consecutive age intervals of 16 weeks length each, according to mating season and sex.

		Age interval in weeks*)					
Term	Level	0-16	16-32	32-48	48-64	64-80	80-96
Mating season	1	59.0^{a} (7.5)	58.0^{a} (7.1)	46.5^{a} (7.1)	40.5^{ac} (7.4)	21.8^{a} (8.1)	26.2 (11.3)
	2	70.0 (7.6)	56.0^{a} (7.1)	47.2^{a} (7.1)	-2.2^{b} (7.4)	55.0^{b} (9.3)	-3.2 (11.3)
	3	83.3^{b} (7.4)	51.7^{a} (7.0)	32.0^{b} (7.0)	27.5^{a} (7.2)	17.0^{ac} (8.3)	22.4^{a} (8.8)
	4	82.9^{b} (7.23)	46.2^{a} (7.0)	7.6^{c} (7.0)	56.2^{c} (7.5)	36.0^{ab} (7.8)	-6.6^{b} (9.6)
	5	82.4^{b} (7.5)	27.0^{b} (7.1)	35.6^{ab} (7.1)	39.0^{a} (7.6)	19.8^{ac} (8.0)	17.5 (9.6)
	6	74.6 (7.8)	14.6^{b} (7.7)	45.6^{ab} (7.9)	31.6^{a} (8.4)	-7.7^{c} (10.4)	34.9 (15.0)
Sex	females	70.2^{a} (6.7)	40.2^{a} (6.5)	35.5 (6.5)	32.4 (6.6)	23.1 (6.9)	12.4 (7.9)
	males	80.5^{b} (6.7)	44.2^{b} (6.6)	35.9 (6.6)	31.8 (6.6)	24.2 (7.0)	17.9 (7.7)

*) Factor level estimates for a given age interval without common letters in their superscripts differed at the five percent level of significance.

Overall average daily weight gains from birth until 48 weeks and from 48 to 96 weeks did not differ significantly across mating season groups. Similar performances until 48 weeks of age were observed in groups 1 to 3, and in groups 4 to 6. On average, rates of weight gain were about 11 percent lower in the latter three groups (46 versus 56 $g \cdot day^{-1}$). Beyond one year of age, growth rates reduced to values between 20 and 30 $g \cdot day^{-1}$. Average daily gains of male kids were significantly higher than those of female kids until about 32 weeks of age. Slightly higher gains in females than males were observed between 48 and 64 weeks, though the difference was not significant. Thereafter, the trend was reversed and, again, males grew faster than females.

Body weight of kids

Statistics that summarize important features of the analysis of kid body weights until two years of age are given in Table 4.6. The dam and kid variance components were found to be nonsignificant. The influences of milk yield until weaning and litter size on weight development of kids were assessed in a separate model, since these effects were confounded with those of mating season and parity. The production cycle variance component and its interaction with the mating season treatment effect had a highly significant influence on model predictions. In both models fitted these sources of variation were small. However, it should be emphasized that they represent deviations of the intercepts of (production cycle specific) response profiles from the population mean intercept, i.e. the population mean birth weight, which itself is small in magnitude and has a smaller variance compared to body weight estimates at later ages, as is apparent from age-specific variance estimates given in Table 4.6.

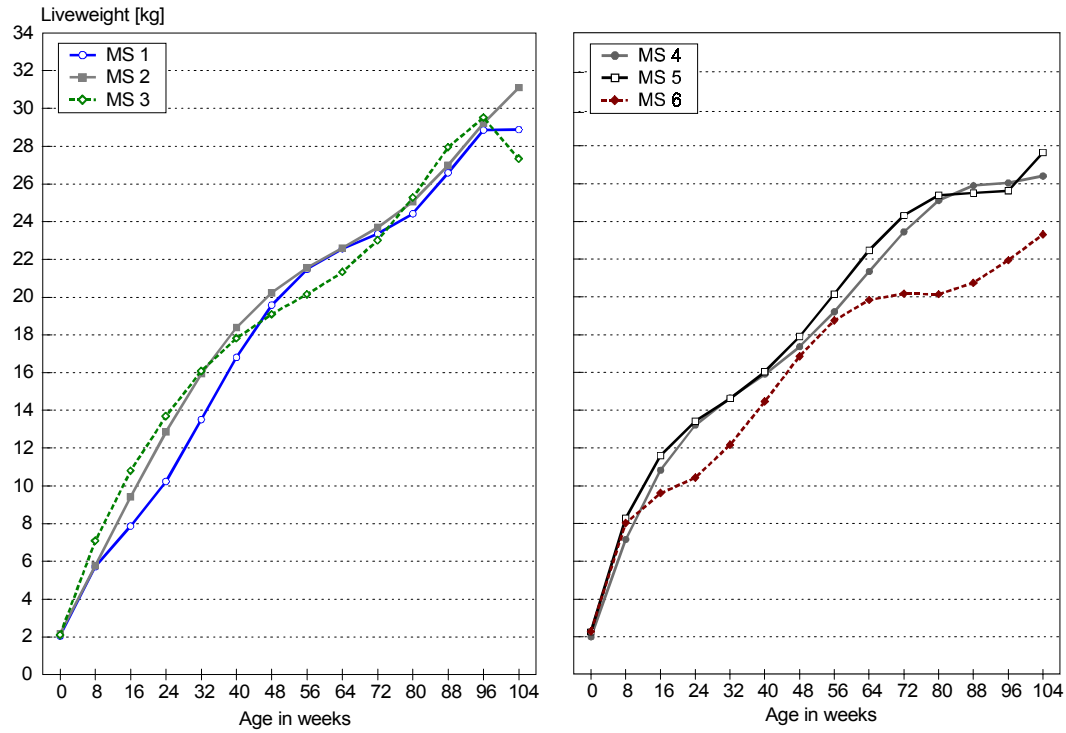

Figure 4.4. Estimated growth curves (least squares means) of kids by mating season group (MS).

Estimated growth curves by mating season, milk yield until weaning, and litter size are depicted in Figures 4.4 and 4.5. Corresponding least squares means and their associated standard errors at selected ages are given in Table 4.7. There was no significant effect of mating season on birth weights. However, does joined during the long dry season in August/September (group 4) gave birth to the lightest kids, whereas kids born to does that were joined at the beginning or end of the short rains (groups 5 and 6) were about 12 percent heavier. Being weaned at the end of the long dry season, kids in the former group were also more than 30 percent lighter at 16 weeks of age than those weaned at the end of the long rains (group 5). As was already indicated by the differences in relative growth rates reported above, maximum weaning weights were generally achieved when suckling took place between end of October and end of June (groups 3 to 5). However, the response profiles in Figure 4.4 show that any disadvantages of low birth and weaning weights incurred by kids in the first two mating season groups were more than offset during a phase of intensive growth observed between weaning and one year of age.

Body weight estimates in Table 4.7 indicate that by 56 weeks, relative differences across mating season groups had considerably diminished. At this age, the largest difference observed was between animals in group 2 and those in group 6, the former being heavier by 2.8 kg or 13 percent. This trend persisted at later ages and, consequently, body weights did not differ significantly between groups 1 to 5 until 88 weeks. In contrast, offspring in mating season 6 never recovered from the nutritional constraints experienced shortly after weaning and, beyond one year of age, had considerably lower liveweights than animals in all other treatment groups. At two years of age, the discrepancy of body weight in group 6 animals compared to others ranged from 3.1 kg (13%, group 4) to a as much as 7.8 kg (33%, group 2).

First parity young weighed significantly less at birth than second parity young, and continued to do so up to 24 weeks of age ($p< 0.05$). Polynomial contrasts revealed a significant cubic trend at birth ($p< 0.05$), and significant linear and quadratic trends ($p< 0.01$) at all later ages in body weights with increasing parity of dam. Kids born to does with at least four prior kiddings grew markedly slower and were lighter from 8 weeks onwards than lower parity kids. Fourth and greater parity young were 4, 14, and 19 percent lighter at birth, one and two years of age, respectively, than second born young which displayed the best overall growthperformance.

Sexual dimorphism in body weights was considerable and became more pronounced with advancing age. The male to female weight ratio increased from 1.05 at birth to 1.13 and 1.17 at one and two years of age. Single born kids were found to be significantly heavier at all ages than twin born kids. The discrepancy in body weight in twin kids initially increased from 7 percent at birth to 22 percent at weaning, but then, due to a faster postweaning growth rate in single kids, reduced to 14 percent by one year of age. Referring to the

estimated body weights at two years of age, litter size had a substantial effect on growth performance; surviving singles being heavier than twins by almost 4 kg. Despite their superior postweaning growth performance, twin born did not fully compensate for their lower initial birth weight and growth intensity.

Table 4.6. Tests of fixed effects and estimates of variance components and covariance parameters for growth curve models fitted to kid body weights from birth to two years of age, accounting for the effects of ***a)*** mating season, parity and sex, and ***b)*** milk yield until weaning, litter size and sex.

	a)				*b)*		
Fixed effects	*df*	χ^2	$p>\chi^2$	*Fixed effects**)	*df*	χ^2	$p>\chi^2$
Mating season	5	81.9	<0.001	MILK16	4	103.6	<0.001
Parity	4	18.9	0.001	Littersize	1	154.3	<0.001
Sex	1	51.9	<0.001	Sex	1	72.7	<0.001
t	1	4489.3	<0.001	t	1	5521.7	<0.001
t^2	1	275.5	<0.001	t^2	1	288.2	<0.001
t^3	1	50.6	<0.001	t^3	1	49.3	<0.001
t^4	1	43.3	<0.001	t^4	1	36.7	<0.001
t^5	1	5.3	0.021	t^5	1	7.4	0.007
t^6	1	9.5	0.002	t^6	1	15.8	<0.001
t×matingseason	5	43.9	<0.001	t×MILK16	4	7.3	0.123
t^3×matingseason	5	23.9	0.016	t^2×MILK16	4	19.3	0.001
t^4×matingseason	5	88.0	<0.001	t^3×MILK16	4	20.8	<0.001
t^5×matingseason	5	78.1	<0.001	t^4×MILK16	4	29.2	<0.001
t^6×matingseason	5	57.7	<0.001	t×littersize	1	7.2	0.007
t×parity	4	16.9	0.002	t^2×littersize	1	10.0	0.002
t×sex	1	24.7	<0.001	t^3×littersize	1	14.3	<0.001
				t×sex	1	43.6	<0.001

*Within-subject covariance parameters***)	*age* [*weeks*]	*estimate*	*std. error*	*Within-subject covariance parameters***)	*age* [*weeks*]	*estimate*	*std. error*
ρ		0.83	0.01	ρ		0.76	0.01
σ^2	0	0.22	0.02	σ^2	0	0.21	0.01
	8	4.97	0.35		8	3.65	0.26
	16	6.68	0.49		16	4.87	0.36
	24	7.27	0.55		24	5.82	0.45
	32	9.94	0.77		32	8.26	0.65
	40	10.90	0.86		40	9.50	0.76
	48	13.58	1.10		48	11.96	0.98
	56	17.46	1.45		56	14.49	1.23
	64	18.20	1.58		64	14.29	1.28
	72	17.00	1.58		72	14.03	1.37
	80	17.21	1.75		80	13.96	1.51
	88	17.57	1.96		88	13.82	1.65
	96	21.59	2.83		96	16.81	2.38
	104	20.54	3.21		104	17.31	2.88

Variance components			*Variance components*		
$\sigma^2_{PC\times MS}$	0.046	0.015	σ^2_{PC}	0.0039	0.0036

*) MILK16=milk yield until weaning.

**) ρ=autoregressive parameter standing for the correlation between adjacent observations on the same subject; σ^2=variance of an observation at a given age; PC=production cycle; MS=mating season. Note that standard errors for variance components are based on asymptotic normality.

Table 4.7. Least-squares means and standard errors (in parentheses) of kid body weights at selected ages, according to mating season, litter size, sex, and milk yield until weaning.

		Age in weeks*)			
Term	Level	0	16	56	104
Mating season	1	2.0 (0.14)	7.9^{a} (0.35)	21.5^{a} (0.57)	28.9^{ab} (1.10)
	2	2.2 (0.14)	9.4^{a} (0.39)	21.6^{a} (0.58)	31.1^{ab} (1.13)
	3	2.1 (0.14)	10.8^{b} (0.36)	20.1 (0.52)	27.3^{b} (0.95)
	4	2.0 (0.14)	10.8^{b} (0.33)	19.2^{b} (0.49)	26.4^{ac} (0.94)
	5	2.3 (0.14)	11.6^{b} (0.40)	20.2 (0.57)	27.7^{ac} (1.09)
	6	2.3 (0.17)	9.6^{b} (0.44)	18.8^{b} (0.86)	23.3^{c} (1.79)
Doe parity	0	2.0^{a} (0.07)	10.0^{a} (0.20)	20.3 (0.46)	27.8 (0.94)
	1	2.2^{b} (0.07)	10.5^{b} (0.19)	21.6^{a} (0.46)	29.8^{a} (0.89)
	2	2.1 (0.07)	10.1 (0.19)	20.6^{a} (0.43)	28.1^{a} (0.88)
	3	2.1 (0.07)	10.0^{a} (0.20)	20.2 (0.47)	27.3 (0.92)
	≥4	2.1 (0.09)	9.5^{a} (0.25)	18.5^{b} (0.67)	24.2^{b} (1.30)
Sex**)	females	2.1^{A} (0.06)	9.6^{A} (0.17)	19.0^{A} (0.33)	25.3^{A} (0.73)
	males	2.2^{B} (0.06)	10.4^{B} (0.17)	21.4^{B} (0.35)	29.6^{B} (0.72)
Milk yield (kg)	<22.5	2.0^{a} (0.07)	7.6^{a} (0.30)	20.1 (0.55)	28.7 (1.60)
	22.5 to 32.5	2.1 (0.06)	10.2^{b} (0.27)	20.4 (0.45)	28.4 (1.20)
	32.5 to 42.5	2.1 (0.07)	10.2^{b} (0.30)	20.4 (0.51)	27.9 (1.20)
	42.5 to 52.5	2.2^{b} (0.07)	11.0^{b} (0.27)	21.0 (0.44)	29.3 (0.96)
	≥52.5	2.3^{b} (0.07)	12.1^{c} (0.26)	21.6 (0.44)	27.0 (1.45)
Litter size	singles	2.2^{A} (0.05)	11.2^{A} (0.19)	22.0^{A} (0.33)	30.1^{A} (0.81)
	twins	2.1^{B} (0.05)	9.2^{B} (0.17)	19.3^{B} (0.30)	26.4^{B} (0.78)

*) Factor level estimates for a given age without common letters in their superscripts differed at the five (lower case letters) or one percent (upper case letters) level of significance.

**) Estimates based on model *a)* in Table 4.6.

The amount of milk available to kids during the suckling period had a marked effect on their body weight development up to about one year of age. Thereafter, patterns became inconsistent and, by 96 weeks of age, differences due to milk yield of dam until weaning failed to reach statistical significance. Does with poor milk yields until weaning (< 22.5 kg) gave birth to the lightest kids, whereas kids born to does producing more than 52.5 kg milk were approximately 16 percent heavier than the latter. Polynomial contrasts revealed a significant ($p< 0.01$) linear trend in birth weights with increasing milk yield level. At later ages up to 32 weeks, a significant ($p< 0.01$) quadratic trend component was also detected. From the body weight estimates in Table 4.7, it is evident that after 56 weeks surviving kids in the lowest milk yield class had almost fully compensated for their poor preweaning growth performance. By two years of age, body weight differences across milk yield levels did not exhibit any systematic pattern.

4.3.2 Doe liveweight

Statistics summarizing important features of the analysis of liveweight development of does over a reproductive cycle of one year duration are presented in Table 4.8. This response was modelled as a polynomial spline function in time differing according to mating season and parity. The spline function consisted of a fourth degree base function, and a cubic segment joining at synchronized week 20, coinciding with the beginning of the recording period immediately preceding parturition. The inclusion of the linear trend component $(t\text{-}20)_{+}$ allowed the introduction of a discontinuity into the response curves and thus to

accommodate for the characteristic decline in body weights observable immediately after parturition. A significant part of the variation in liveweights was due to the random effect of production cycle and to its interaction with the mating season treatment variable ($p< 0.01$). In contrast, the subject variance component was found a nonsignificant source of variation ($p>0.20$).

Results of the model fitted to the percent change in individual liveweights at each time point relative to that measured 22 weeks prepartum (corresponding to the approximate time at conception) are given in Table 4.9. As before, mating season and parity stage were found to have a systematic effect on outcomes. Also, the effect of mating season on relative weight changes varied substantially across production cycles, as is apparent from the comparatively large (and highly significant, $p< 0.001$), mating season×production cycle component of variance. As it was set to zero by the REML estimation procedure, the random production cycle effect was dropped from the final model.

The effects of lagged median range condition scores [I] and [II] at each time point were statistically significant, but the respective estimated response profiles did not lend themselves to a meaningful interpretation,

Table 4.8. Tests of fixed effects and estimates of variance components and covariance parameters for growth curve models fitted to liveweights of fertile does, accounting for the effects of mating season and parity.

*Fixed effects**)*	*df*	χ^2	$p>\chi^2$
MS	5	18.1	0.003
Parity	3	587.7	0.000
t	1	46.3	<0.001
t^2	1	27.0	<0.001
t^3	1	307.6	<0.001
t^4	1	4.1	0.043
(t-20)+	1	331.7	<0.001
$(t-20)^2+$	1	137.0	<0.001
$(t-20)^3+$	1	61.4	<0.001
t×MS	5	17.5	0.004
t^2×MS	5	52.1	<0.001
t^3×MS	5	29.4	<0.001
t^4×MS	5	102.2	<0.001
(t-20)+×MS	5	11.6	0.041
$(t-20)^2+$×MS	5	45.1	<0.001
$(t-20)^3+$×MS	5	36.2	<0.001
t×parity	3	35.0	<0.001
t^2×parity	3	12.8	0.005
(t-20)+×parity	3	12.5	0.006

Variance components	*estimate*	*std. error*
σ^2_{PC}	2.10	1.67
$\sigma^2_{PC\times MS}$	1.14	0.48

*Covariance parameters***)	*time (weeks)*	*estimate*	*std. error*
ρ		0.85	0.01
σ^2	0	13.0	0.98
	2	13.8	0.97
	4	12.1	0.85
	6	13.1	0.92
	8	19.3	1.37
	10	21.1	1.49
	12	21.8	1.55
	14	23.4	1.66
	16	21.1	1.50
	18	23.7	1.68
	20	30.3	2.14
	22	49.3	3.50
	24	22.1	1.57
	26	19.3	1.37
	28	17.1	1.22
	30	17.4	1.24
	32	15.3	1.10
	34	15.2	1.10
	36	15.7	1.14
	38	16.6	1.22
	40	18.2	1.35
	42	14.9	1.11
	44	15.1	1.14
	46	13.3	1.02
	48	16.0	1.25
	50	16.6	1.36
	52	16.1	1.55

*) MS=mating season.

**) ρ=autoregressive parameter standing for the correlation between adjacent observations on the same subject; σ^2=variance of an observation in a given time interval; PC=production cycle. Note that standard errors for variance components are based on asymptotic normality.

and therefore both effects were omitted from consideration. Since type of birth was confounded with mating season and dam parity stage, its effect on liveweight development of fertile does was studied separately. The approach followed was to include parity and its interaction with litter size as explanatory factors into the model, and then to obtain simple effects response curves for does with single and twin birth events within each parity class. Liveweight development was again assessed both in absolute and in relative terms, and statistical summaries of this part of the analysis are presented in Table 4.10.

Table 4.9. Tests of fixed effects and estimates of variance components and covariance parameters for growth curve models fitted to percent change in liveweights of fertile does, accounting for the effects of mating season and parity.

*Fixed effects**)*	*df*	χ^2	$p>\chi^2$
MS	5	4.0	0.557
Parity	3	121.8	<0.001
t	1	73.9	<0.001
t^2	1	39.5	<0.001
t^3	1	455.7	<0.001
t^4	1	56.1	<0.001
(t-20)+	1	359.9	<0.001
$(t-20)^2+$	1	119.8	<0.001
$(t-20)^3+$	1	72.6	<0.001
t×MS	5	23.9	<0.001
t^2×MS	5	104.0	<0.001
t^3×MS	5	51.3	<0.001
t^4×MS	5	114.0	<0.001
(t-20)+×MS	5	24.0	<0.001
$(t-20)^2+$×MS	5	70.4	<0.001
$(t-20)^3+$×MS	5	42.1	<0.001
t×parity	3	61.2	<0.001

Variance components	*estimate*	*std. error*
σ^2PC×MS	126.6	37.8

*Covariance parameters***)	*time (weeks)*	*estimate*	*std. error*
ρ		0.75	0.01
σ^2	2	70.7	5.60
	4	54.5	4.00
	6	57.0	4.19
	8	98.8	7.27
	10	103.0	7.59
	12	111.3	8.20
	14	116.7	8.59
	16	103.0	7.59
	18	116.3	8.56
	20	151.9	11.10
	22	334.9	24.60
	24	110.2	8.15
	26	117.9	8.72
	28	87.3	6.47
	30	101.7	7.55
	32	82.6	6.17
	34	81.2	6.09
	36	84.2	6.40
	38	108.2	8.31
	40	118.0	9.17
	42	109.4	8.58
	44	91.9	7.31
	46	86.8	7.04
	48	84.5	7.03
	50	105.6	9.26
	52	115.9	12.16

*) MS=mating season.

**) ρ=autoregressive parameter standing for the correlation between adjacent observations on the same subject; σ^2=variance of an observation in a given time interval; PC=production cycle. Note that standard errors for variance components are based on asymptotic normality.

Table 4.10. Tests of fixed effects and estimates of variance components for growth curve models fitted to ***a)*** liveweights and ***b)*** relative changes in liveweight of fertile does, accounting for the effects of litter size and parity at breeding. A heterogeneous first-order autoregressive covariance structure was used in fitting both models. Within-subject covariance parameter estimates were very similar to those presented in Tables 4.8 and 4.9.

	a)				***b)***		
Fixed effects[*)]	*df*	χ^2	$p>\chi^2$	*Fixed effects*[*)]	*df*	χ^2	$p>\chi^2$
LS	1	99.3	<0.001	LS	1	13.6	<0.001
Parity	3	509.4	<0.001	Parity	3	13.4	0.004
LS×parity	3	12.9	0.005	LS×parity	3	8.5	0.037
t	1	40.5	<0.001	t	1	26.4	<0.001
t^2	1	26.8	<0.001	t^2	1	18.4	<0.001
t^3	1	276.3	<0.001	t^3	1	273.1	<0.001
t^4	1	3.5	0.061	t^4	1	39.5	<0.001
$(t-20)_+$	1	344.3	<0.001	$(t-20)_+$	1	259.2	<0.001
$(t-20)^2_+$	1	127.5	<0.001	$(t-20)^2_+$	1	93.4	<0.001
$(t-20)^3_+$	1	62.4	<0.001	$(t-20)^3_+$	1	58.4	<0.001
t×LS×parity	7	43.2	<0.001	t×LS×parity	7	44.4	<0.001
t^2×LS×parity	7	12.1	0.097	t^2×LS×parity	7	10.2	0.180
t^3×LS×parity	7	25.7	0.001	$(t-20)_+$×LS×parity	7	14.5	0.043
$(t-20)_+$×LS×parity	7	15.3	0.033				
$(t-20)^2_+$×LS×parity	7	27.5	<0.001				
Variance components[**)]		*estimate*	*Std. error*				
$\sigma^2_{PC\times MS}$		2.60	1.89				

*) LS=litter size.

**) PC=production cycle. Note that the standard error for the variance component is based on asymptotic normality.

Plots of predicted doe liveweights by mating season group and parity from 20 weeks prior to parturition up to 30 weeks postpartum, the approximate time at which rebreeding would be expected to take place under seasonal breeding management, are given in Figure 4.5. Note that estimates for synchronized week 20 and 24 correspond to predicted pre- and postpartum liveweights of dams. Least squares means and standard errors of liveweights by mating season and parity and percent changes therein at selected stages are presented in Tables 4.11 and 4.12. Liveweights of does at the time of conception did not differ substantially across mating seasons, except for group 6, in which does were markedly lighter than in all other groups. However, this result may have been biased due to the smaller number of observations in group 6 and due to the fact that a very largeproportion (72 percent) of the does joined in this group have had a live birth event within 40 weeks prior to mating. For comparison, figures for groups 1 to 5 amounted to, respectively, 26, 26, 47, 63, and 33 percent of the does joined. As expected, increases in liveweights during pregnancy, adjusted for the effect of parity, were largest (>32 percent increase relative to liveweight at conception) when mating took place at the beginning or just prior to the rainy seasons (groups 5 and 6), so that during most of the pregnancy stage animals were exposed to favourable forage conditions. Conversely, liveweight gains decreased gradually the further the pregnancy stage was displaced towards the long dry season (groups 1 to 3). At the measurement time immediately preceding parturition (synchronized week 20), the heaviest dams were observed in mating season group 1 (42 kg), and the lightest in mating season group 3 (38 kg), although differences in liveweight reached statistical significance only during the postpartum period. Weight losses between pre- and postpartum measurement times varied only slightly and ranged from 4.9 (group 4) to 6.4 kg (group 6). The average change in liveweight in the various groups during the suckling period (differences between week 24 and 38) ranged from a weight loss of 4.9 kg in group 1 to a weight gain of 2.2 kg in group 3.

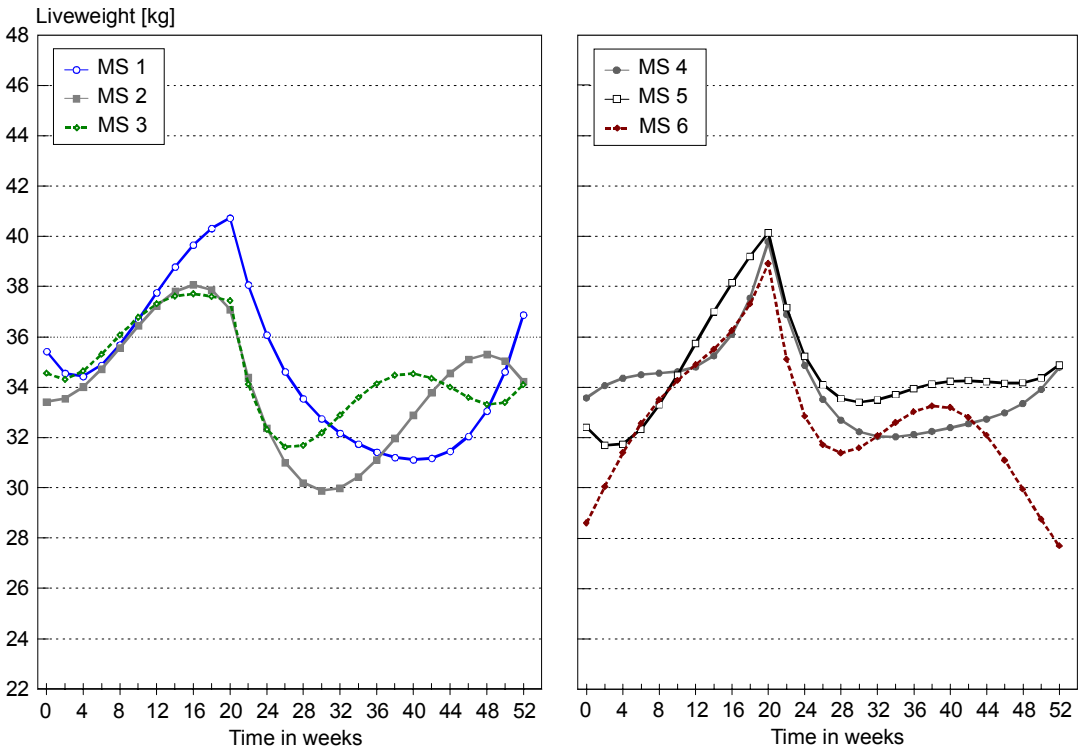

Figure 4.5. Estimated growth curves (least squares means) of does by mating season over a reproductive cycle of one year duration. The time origin corresponds approximately to the date at conception.

Table 4.11. Least-squares means and standard errors (in parentheses) of liveweight of fertile does (kg) at selected time points during a reproductive cycle of one year duration, according to mating season and parity at breeding.

		time in weeks*)									
Term		0		20		24		38		52	
Mating	1	35.4^{a}	(1.16)	42.0	(1.43)	36.1^{a}	(1.18)	31.2	(1.16)	36.9^{a}	(1.24)
season	2	33.4^{a}	(1.18)	38.0	(1.46)	32.4^{b}	(1.21)	32.0	(1.18)	34.2^{a}	(1.28)
	3	34.5^{a}	(1.19)	38.1	(1.46)	32.3^{b}	(1.22)	34.5	(1.19)	34.1^{a}	(1.29)
	4	33.6^{a}	(1.17)	39.7	(1.45)	34.9	(1.20)	32.2	(1.17)	34.8^{a}	(1.34)
	5	32.4	(1.21)	40.5	(1.49)	35.2	(1.24)	34.1	(1.21)	34.9	(1.37)
	6	28.6^{b}	(1.33)	39.3	(1.66)	32.8	(1.36)	33.3	(1.32)	27.7^{b}	(1.41)
Parity	0	25.4^{a}	(1.00)	31.2^{a}	(1.07)	27.1^{a}	(1.00)	27.9^{a}	(0.98)	28.3^{a}	(1.07)
	1	32.9^{b}	(0.99)	38.8^{b}	(1.06)	33.7^{b}	(0.99)	32.9^{b}	(0.98)	35.0^{b}	(1.07)
	2	36.2^{c}	(1.00)	42.1^{c}	(1.07)	36.7^{c}	(1.00)	34.9^{c}	(0.98)	35.8^{b}	(1.07)
	≥3	37.6^{c}	(1.01)	43.8^{c}	(1.09)	38.3^{c}	(1.01)	35.9^{c}	(1.00)	35.9^{b}	(1.11)

*) Factor level estimates for a given time point without common letters in their superscripts differed at the five percent level of significance.

Table 4.12. Least-squares means and standard errors (in parentheses) of relative liveweight change (%) in fertile does from date at conception until selected time points during a reproductive cycle of one year duration, according to mating season and parity at breeding.

		time in weeks*)			
Term	Level	20	24	38	52
Mating season	1	18.6 (6.68)	4.5 (6.62)	-7.4 (6.61)	8.4 (6.76)
	2	12.7 (6.72)	-1.0 (6.65)	-3.6 (6.63)	2.7 (6.82)
	3	12.1 (6.73)	-2.9 (6.66)	4.7 (6.64)	5.7 (6.84)
	4	20.8 (6.70)	7.3 (6.64)	-0.9 (6.62)	5.8 (6.93)
	5	32.2 (6.77)	14.9 (6.68)	12.4 (6.66)	11.7 (6.97)
	6	37.8 (8.21)	16.9 (8.12)	16.2 (8.10)	-2.4 (8.26)
Parity	0	26.2^{A} (2.90)	11.2^{A} (2.87)	10.8^{A} (2.89)	15.2^{A} (3.06)
	1	23.7^{B} (2.90)	8.2^{B} (2.87)	5.9^{B} (2.89)	8.4^{B} (3.06)
	2	20.6^{C} (2.90)	4.6^{C} (2.87)	0.5^{C} (2.90)	1.1^{C} (3.06)
	≥3	19.0^{C} (2.91)	2.6^{C} (2.88)	-2.8^{D} (2.91)	-3.4^{D} (3.11)

*) Factor level estimates for a given time point without common letters in their superscripts differed at the five percent (lower case letters) or one percent (upper case letters) level of significance.

Although differences across mating season groups in liveweights and the associated relative changes therein failed to reach significance during lactation, it is nevertheless clear that mobilization of body reserves was more pronounced when the lactation stage coincided with periods of low quality and quantity of forage on offer (groups 1 and 2) than with periods of good pasture availability (groups 4, 5, and 6). The response profiles in Figure 4.5 show that liveweight recovery in does joined in mating seasons 1, 2 and 3 was linked to the onset of the short rainy season, which occurred at a very late stage for group 1 (around week 46) and shortly after birth for group 3. Weight losses during early lactation were much smaller in groups 4 to 6, and at weaning time, slight relative weight losses could only be observed in group 4 (-0.9 percent). Does in mating season group 5 and 6 were still more than 12 percent heavier at weaning than at conception time. In response to the favourable feeding conditions prevailing throughout the long rains, a steady increase in body weights was observed in mating seasons 4 and 5 from 32 weeks onwards. Although does in mating season 6 were on average only about 0.5 kg lighter at weaning than at the postpartum measurement time, liveweight losses during the following long dry season were substantial, amounting to approximately 5.5 kg, such that animals were predicted to weigh slightly less after 52 weeks than at conception (-2.4 percent).

Except for mating season group 6, breeding does generally were able to fully replenish their body reserves by 52 weeks. The relative increases in liveweight of 3 to 12 percent (Table 4.13) in mating seasons 1 to 5 also indicate that, on average, immature females must have achieved net growth in body weight over the reproductive cycle. This is also apparent from the response profiles by parity class shown in Figure 4.6 and the corresponding estimated relative weight changes given in Table 4.13. First kidding does were significantly lighter at all measurement times, but also achieved much larger relative weight gains during the reproductive cycle than higher parity does. Relative weight changes decreased linearly ($p< 0.001$) with increasing parity of does at all stages. While first kidding does on average had gained 2.9 kg (15.2 percent) by 52 weeks, third and higher parity does were on average 1.7 kg (-3.4 percent) lighter at that stage than at conception time. Does with one and two prior kiddings were on average 2.1 (8.4 percent) and 0.4 kg (1.1 percent) heavier after completing the reproductive cycle. From 28 weeks onwards, all pairwise comparisons of estimated relative weight changes by parity stage were highly significant.

Litter size exerted a marked influence on liveweight development of does, although this effect was not constant across parity levels (Figure 4.6 and Tables 4.13 and 4.14). At conception time, there was a slight tendency for higher liveweights in does carrying twin fetuses, the difference to does carrying a single fetus ranging from 0.6 kg (at least three prior kiddings) to 1.6 kg (two prior kiddings). Does carrying twin fetuses were not generally heavier at, and did not generally exhibit higher relative weight changes until the end of the gestation period than those carrying a single fetus. This was the case only in parity one and two does, which were predicted to be heavier by, respectively, 4 kg (10.7 percent) and 5.2 kg (13.2 percent) at 20 weeks from conception. The reverse was observed in nulliparous and third and higher parity animals, though here the estimated liveweight differences between those carrying single and twin fetuses were very small (1.3 and 1.8 percent, respectively).

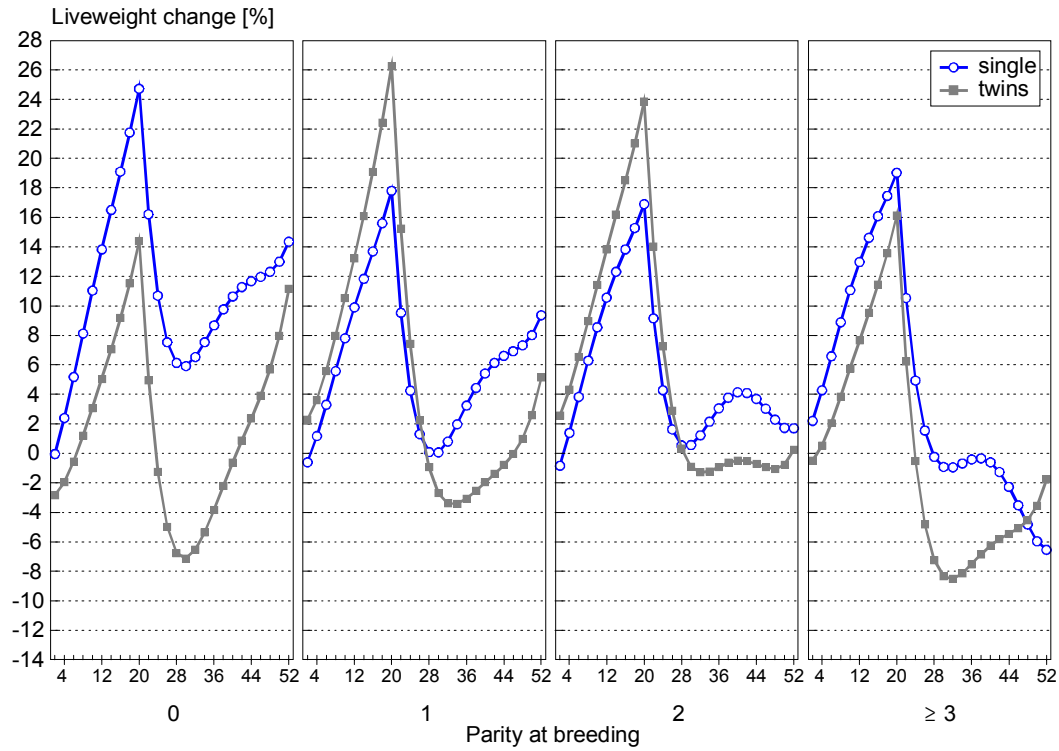

Figure 4.6. Estimated simple effects of litter size within parity class on relative liveweight change in does over a reproductive cycle of one year duration. The time origin corresponds approximately to the date at conception.

Table 4.13. Least-squares means and standard errors (in parentheses) of liveweights (kg) of fertile does at selected time points during a reproductive cycle of one year duration, according to litter size and parity at breeding.

Term			time in weeks*) 0	20	24	38	52
Parity	0	single	25.6 (1.08)	31.8 (1.12)	28.0 (1.07)	27.7 (1.05)	29.2 (1.20)
		twins	27.0 (1.56)	31.4 (1.71)	26.3 (1.51)	26.3 (1.43)	30.6 (1.83)
	1	single	32.7 (1.11)	37.4^{a} (1.17)	33.7 (1.10)	33.3 (1.08)	35.7 (1.25)
		twins	33.7 (1.30)	41.4^{b} (1.40)	35.2 (1.27)	31.6 (1.23)	33.5 (1.57)
	2	single	35.3 (1.21)	39.4^{a} (1.29)	35.0 (1.19)	34.9 (1.15)	34.7 (1.37)
		twins	36.9 (1.18)	44.6^{b} (1.25)	37.3 (1.16)	35.4 (1.13)	35.1 (1.33)
	≥3	single	38.0 (1.32)	44.5 (1.42)	39.5 (1.28)	38.0^{a} (1.24)	35.9 (1.57)
		twins	38.6 (1.14)	43.7 (1.20)	37.8 (1.13)	34.7^{b} (1.11)	37.0 (1.34)

*) Factor level estimates within parity classes at each time point without common letters in their superscripts differed at the five percent level of significance.

Table 4.14. Least-squares means and standard errors (in parentheses) of relative liveweight change (%) of fertile does at selected time points during a reproductive cycle of one year duration, according to litter size and parity at breeding.

Term			time in weeks*) 20		24		38		52	
Parity	0	single	24.7	(2.19)	10.7^{a}	(1.75)	9.8^{a}	(1.68)	14.3	(2.13)
		twins	14.4	(4.95)	-1.3^{b}	(3.90)	-2.2^{b}	(3.70)	11.1	(4.50)
	1	single	17.8	(2.44)	4.2	(1.94)	4.4	(1.86)	9.4	(2.35)
		twins	26.3	(3.61)	7.4	(2.84)	-2.5	(2.73)	5.1	(3.60)
	2	single	16.9	(3.08)	4.3	(2.44)	3.8	(2.34)	1.7	(2.85)
		twins	23.8	(2.88)	7.2	(2.29)	-0.6	(2.21)	0.2	(2.69)
	≥3	single	19.0	(3.70)	4.9	(2.92)	-0.4	(2.79)	-6.5	(3.58)
		twins	16.1	(2.64)	-0.5	(2.10)	-6.9	(2.05)	-1.8	(2.72)

*) Factor level estimates within parity classes at each time point without common letters in their superscripts differed at the five percent level of significance.

Relative decreases in liveweights between pre- and postpartum measurement times varied only slightly across parity stages, and ranged from 10.9 to 11.8 percent in does that gave birth to a single kid, and from 13.5 to 16.4 percent in does with twin birth events. However, as may be seen from the response profiles in Figure 4.6, the depression in liveweights during lactation was much larger in does nursing twins, which in all parity stages exhibited net relative weight losses until weaning. This pattern was most pronounced in third and greater parity animals, with an average reduction in liveweight until weaning of 6.9 percent relative to that observed at conception time. In contrast, does nursing singles never exhibited net relative weight losses during the lactation stage except for parity class three and greater, in which dams were predicted to be about 6 percent lighter by the end of the reproductive cycle than at the time of conception. The sharp decline beyond 40 weeks in the latter curve of liveweight change, however, was related to both the small number of observations in this cell of the design from 44 weeks onwards (< 15 observations) and to the absence of a control for environmental influences on responses in the fitted model. For instance, for ten out of the fifteen parity three or greater does nursing a single kid, the end of the lactation stage coincided with the long dry season.

4.4 Discussion

4.4.1 Growth performance of kids

Effects of sex, litter size, milk yield, and parity of dam

Consistent with expectation, sex and litter size exerted significant effects on birth weights and subsequent growth rates, with females weighing less than males, and twins less than singles. An interesting feature of the analysis is that relative growth rates, expressed as weight gain per day relative to average metabolic body weight, of female and male kids did not differ significantly from each other. This points to the fact that deviations in absolute growth rate (AGR) were entirely due to the larger birth and mature weight of males, and not to differences in growth intensity or maturing rate. Hence, upon expressing AGR in relation to average metabolic body weight status, size-dependent effects on observed growth performance tend to be reduced or eliminated. A similar conclusion could have been arrived at by using the relative growth rate measure (RGR) suggested by Fitzhugh and Taylor (1971), defined as the difference between the natural logarithm of two consecutive weight measurements divided by the length of time interval, which represents the average percentage change in body weight per day. As indicated by Fitzhugh (1976), RGR may also be approximated by AGR/$[(y_{t+1}+y_t)/2]$, where y_{t+1} and y_t are body weight measurements made at two consecutive time points; the only difference between this and the measure employed in the present study is that the denominator (average body weight) is not converted to the metabolic weight scale. Consequently, at any age, there was an almost perfect correlation (r>0.99) between the index used in the present analysis and RGR as defined by Fitzhugh and Taylor (1971).

In contrast to the effect of sex, litter size affected both intercepts and shapes of growth curves, such that twins were not only lighter at birth, but also matured at a slower rate than singles until approximately 18 weeks of age, while the relationship was reversed thereafter. This pattern was undoubtedly due to the increased competition (at a given yield level) for milk in twin litters, given that the effect of litter size remained unaffected by milk yield level until weaning. Retarded growth caused by suboptimal levels of nutrition during the preweaning period implied that twin born kids were less mature at weaning than singles and this was probably conducive to the faster growth rate observed in surviving twins over subsequent time periods. However, this was not sufficient to fully compensate the difference in body weight, and singles were persistently heavier than twins by about 14 percent from one year of age onwards. Similar differences in body weights between twins and singles have been noted previously by Sacker and Trail (1966), who found single born male and female SEA Mubende goats to be heavier by 17 and 7 percent at one year of age, respectively, compared to their twin born contemporaries.

The observation that birth weights tended to increase with milk yield level until weaning appears to be largely due to the fact that milk yields themselves were found to be strongly correlated with liveweight of does at parturition time. Because of the presence of this collinearity, postpartum dam weight was not considered as a source of variation in analysing body weight development of kids. However, an examination of the effect of dam postpartum weight, adjusted for the effects of sex and litter size, revealed significant linear and quadratic trends ($p< 0.05$) in birth weight with increasing postpartum weight of dam. This is in accordance with previous reports (Amoah et al., 1995; Devendra and Burns, 1983; Sherman, 1987), and with the general principle of productive output being proportional to the metabolic weight of the dam (Taylor and Murray, 1987). But postpartum weight itself may have been influenced by many factors, including degree of maturity, phenotypic variation in size, or nutritional state of dam during pregnancy. Hence, though postpartum dam weight certainly bears some relationship to maternal capacity, its use as a predictor variable probably does little to elucidate the mechanisms by which prenatal environment and maternal factors may affect birth weight of kids.

The effect of total milk yield until weaning on body weight gains followed the expected pattern, in that a clear linear trend in responses with increasing milk availability for youngstock was observed until about 10 weeks of age. This influence decreased steadily with advancing age and, by one year, differences in body weight were largely independent of the amount of milk available until weaning. It is interesting to note that, if they survived, kids which had access to the least amount of milk until weaning were able to compensate for this handicap by a phase of accelerated growth between 3 and 6 months of age. These increased rates of gain suggest that the smaller quantity of milk sucked was possibly compensated for by increased intake of pasture feeds at an early stage of life, so that such animals were effectively weaned and had fully developed rumens well before weaning at 4 months of age.

A curvilinear relationship was detected between dam parity and birth weight of kids, with first and second kidding does giving birth to the lightest and heaviest kids, respectively. At later ages, this pattern changed slightly in that markedly lower body weights were observed for kids born to fourth and higher parity does, relative to all others. However, parity did not affect relative or absolute growth rates, thus complicating the interpretation of the effect of this factor on body weight development of kids. The model used did not account for the effects of litter size and milk yield, since both were correlated with the effects of parity and mating season. Then, a possible explanation for the observed pattern is that the decrease in birth weights and growth rates associated with the higher probability of twin birth events in multiparous does was counteracted, to some extent, by an opposite effect exerted on these traits by the curvilinear trends in dam body weight and milk production with increasing number of lactations. Hence, although birth weights and growth rates could be expected to increase up to the third lactation due to concomitant increases in dam weight and milk yield, this may have been attenuated by the higher probability of producing twins in older does.

Effects of mating season

It is generally accepted that the rapid rate of fetal growth during the final stage of pregnancy imposes a metabolic strain on the doe (Dunn and Moss, 1992; Landau et al., 1996; Sauvant et al. 1991). When the dietary supply of nutrients is inadequate, these increased nutritional requirements are met by mobilising body reserves. Consequently, it has been stated that goats, like other domestic ruminant species (Dunn and Moss, 1992; Spitzer et al., 1995), are sensitive to nutritional stress during pregnancy, especially under extensive management conditions (Sibanda et al., 1997; Osuagwuh, 1992). Severe malnutrition during varying stages of pregnancy appears to exacerbate liveweight losses and increase the risk of reproductive wastage due to abortion, retardation of fetal growth, reduced birth weight, and increased neonatal death rate. Furthermore, periods of severe nutritional stress *pre partum* are likely to affect subsequent levels of milk production, thus further increasing the likelihood of neonatal losses and depressed growth performance.

In the present experiment, pronounced negative energy balances during gestation and, consequently, low birth weights, could be expected to arise in those treatment groups in which either the entire gestation period (mating season group 3), or the early (mating season group 4) or late (mating season group 2) stages thereof occurred during the long dry season, when feed quality and quantity were most limiting. Conversely, the more favourable feeding conditions prevailing between the months of October and April could be expected to lead to improved birth weights when gestation took place during this period, such as it was the case in mating season groups 5 and 6, as well as in group 4 from mid-pregnancy onwards. However, no systematic effect of mating season on birth weights of kids was detected. On the one hand, the large variation in birth weights accounted for by the random interaction effect of mating season with production cycle obviously contributed to the absence of a clear effect of mating season on birth weights. On the other hand, this was also in part due to the fact that litter size, which was correlated with mating season and parity, could not be included in the corresponding statistical model. Birth weights, however, were found to be significantly lower in twins than in singles. Hence, the low birth weight predicted for kids born at the onset of the dry season (mating season group 1) was certainly to some extent related to the larger proportion of twin birth events in this group (58 percent), which was well above that estimated for all other groups (< 48 percent). Inspection of the liveweight development profile during gestation indicated that does in mating season 1 gained on average 18.6 percent in weight until parturition, and exhibited the highest liveweights at mating and prior to parturition. On average, prepartum body weight losses did not occur, suggesting that fetal growth was probably not inhibited through nutritional constraints.

As expected, signs of severe nutritional stress during late pregnancy were apparent in mating season groups 2 and 3, in which does began to loose weight from about 6 weeks prepartum onwards, but this did not seem to have affected birth weights. Experiments previously conducted under controlled environmental conditions also failed to reveal significant effects of dietary treatments during late pregnancy on birth weights in goats. Sibanda et al. (1997) could not detect differential effects of low, medium, and high energy and protein diets fed 7 weeks before parturition to Matebele goats on birth weights. The authors point out that does in the low energy group could have compensated for nutrient deficiency by mobilizing body reserves to ensure development of the fetuses. In this group, net weight losses (about 5.6 percent) were only apparent when comparing liveweights at the onset of the dietary treatment in week 15 of pregnancy and the post-kidding measurement time, but did not occur between 15 and 21 weeks of gestation. In contrast, Osuagwuh (1992), working with West African Dwarf goats, found that underfeeding between 61th and 120th day of pregnancy significantly depressed birth weights and neonatal growth rates, while a reduction in the plane of nutrition during late pregnancy (>120 days) failed to produce similar results. Also, in a study conducted on Alpine goats, dietary energy concentrations ranging from 1.8 to 2.5 $Mcal \cdot kg^{-1}$ DM fed from 90th gestation day onwards did not affect litter weights (Sahlu et al., 1995), suggesting that severe nutritional restrictions during late gestation may be required to deplete body energy stores enough to influence fetal growth.

From these results and from the review presented by Landau et al. (1996), it seems that the clear expression of differential effects of nutritional factors on fetal growth rate and subsequent birth weight is highly dependent upon the severity of under- or overnutrition, as well as upon the duration and the stage of pregnancy over which these changes in nutrient supply are experienced. Obviously, a further complication arises under field conditions in semi-arid climates, where nutrient availability at any time point during gestation is difficult to quantify, since it is not only determined by seasonal fluctuations in primary productivity, but also by random climatic perturbations which occur at varying time scales and may considerably alter seasonal patterns of forage production. This was partly reflected by the large variation in birth weights accounted for by the production cycle×mating season variance component ($\sigma^2_{PC \square MS}=0.046$), as opposed to the estimated variance of birth weights ($\sigma^2=0.015$). Although non-significant, there nevertheless was slight evidence for a tendency of increasing birth weights when gestation took place between October and April (mating seasons 5 and 6), which generally corresponds to the most favourable period in terms of both feed quality and quantity. Inspection of the liveweight development profiles of does from mating to parturition, adjusted for the effect of parity only, revealed that the largest relative liveweight gains during gestation were achieved in the latter two treatment groups (32.2 and 37.8 percent, respectively), as opposed to all other groups (< 21 percent).

The experiment succeeded in demonstrating that significantly different growth rates achieved by kids could be attributed to mating season, and hence season of birth. The range of absolute growth rates among mating season groups of 44 to 57 $g \cdot day^{-1}$ from birth to 48 weeks of age estimated in this study were somewhat higher than the 38.3 g per day from birth to one year of age observed for SEA goats under comparable husbandry conditions by Wilson et al. (1984). The marked differences in growth patterns across mating season groups may largely be explained on the basis of availability of pasture, particularly during the preweaning period. This conclusion is supported by the finding that both range condition scores had significant impacts on estimated relative growth profiles. The highest average preweaning weight gains were achieved by kids born in the period from October to May (mating season groups 3 to 6), while growth

performance was seriously compromised when birth took place at the middle (mating season group 1) and, to a lesser extent, toward the end of the long dry season (mating season group 2). Growth performance until 3 months of age was severely depressed in the former group as pasture conditions deteriorated in the dry season and does could not cover their nutrient requirements for sustained milk production.

When compared on the basis of relative growth rates, the growth performance estimated from the present data is in agreement with that obtained previously for SEA goats by Wilson (1958) until 8 weeks of age (Table 4.15), though in his study kids appeared to be markedly heavier at birth. After allowance has been made for differences in mature size, it can be seen from the same table that comparable early growth rates are also achieved by other small-sized tropical goat breeds. Comparing growth performance among and within breeds and strains on the basis of absolute growth rates clearly is not very meaningful if there are substantial differences in mature size. Generally, absolute growth rates are highly correlated with body size at maturity, which bears no direct relationship with higher biological efficiency (Brown et al., 1976; Dickerson, 1978; Ogink, 1993). For instance, a large European goat breed such as the German Fawn achieves much higher absolute average daily gains than all other breeds listed in Table 4.15. However, most of this difference is probably due to the variation in genetic size at maturity, as indicated by the performance of the German Fawn in terms of average daily gain relative to metabolic liveweight state. When compared on the basis of this criterion, the latter breed does not appear to be superior to the smaller-sized tropical breeds. In fact, German Fawn goats even seem to grow at a slightly slower relative rate than the others over the first weeks of life. Although it cannot be ascertained based on the figures presented in Table 4.15, such a trend would most likely be an expression of the well known negative genetic relationship between size at maturity and earliness of maturing (Fitzhugh and Taylor, 1971; Taylor and Fitzhugh, 1971; Brown et al., 1976; Fitzhugh, 1976). This negative relationship implies that individuals growing to the heaviest mature weight tend to be less mature at a given age or older at a given degree of maturity.

After weaning, environmental conditions continued to have considerable effects on body weights and weight gains over short time periods of time. However, compensatory effects tended to reduce the net effect of environmentally induced fluctuations in availability and quality of nutrition on estimated weight-at-age profiles. Thus, while substantial differences in body weights could be observed at weaning time among mating season groups, these had almost completely disappeared by one year of age, with the exception of kids belonging to mating season group 6. In the latter group, kids weighed on average 9.6 (±0.35) kg at weaning, at which time they passed through a period of severe nutritional stress coinciding with the middle of the long dry season. During the subsequent period from October to May, which may be considered a re-alimentation phase, compensatory gains were noticeably lower than, for instance, in mating season group 1, in which kids were younger and at a lower degree of maturity. Specifically, at the start of the short rainy season in late October, kids in mating season group 1 were on average 16 weeks old and were estimated to weigh 7.9 (±0.35) kg, while those in mating season 6 were on average 24 weeks old and had an average weight of 10.4 (±0.48) kg. The magnitude of compensatory gains have been reported to be highly dependent upon the physiological maturity at the time of re-alimentation after a period of nutritional stress. In a review on this subject, Hogg (1991) concludes that the potential for the greatest compensatory response apparently occurs in animals whose weight is near 25 to 30 percent of mature size, while above and below this weight their potential to respond declines. Kids in group 6 appeared to be close to the upper end of this range at the time of re-alimentation, and this may partially explain their lower response.

Based on the growth and weight-at-age profiles for mating season 6 youngstock (Figures 4.1 and 4.4), it seems that nutritional restriction may have induced a reduction in mature size. However, Ryan (1990) argues that the level and duration of nutritional restriction required to depress mature size may be far more pronounced than those generally associated with the seasonal variations in pasture quality and quantity on offer. Alternatively, it is possible that animals in group 6 would have continued to grow at the slow rates observed during the second year of life and, eventually, would have reached a similar mature weight as those in other groups, though at a much older age. However, these conclusions must remain tentative, since the small number of observations beyond 64 weeks of age clearly affected the estimation of growth rates and weight-at-age curves. For instance, while weight losses were predicted to occur between weeks 88 and 104 in group 6, this was not reflected in the corresponding weight-at-age curve, which indicated increasing weights from 88 to 104 weeks of age.

4.4.2 Body weight development of does

Effects of litter size and parity of dam

As expected, nulliparous dams were still growing and achieved much higher relative weight gains throughout the reproductive cycle than higher parity dams. The estimated liveweight development profiles by parity class indicate that weight gains levelled off approximately at the end of the third lactation, at which stage dams weighed about 36 kg. The average weight range of 27.7 (mating season 6) to 36.9 kg (mating season 1) observed at the end of the reproductive cycle in the present strain of SEA goats appears to be markedly higher than that reported previously by Ruvuna et al. (1991) for the same breed in Western Kenya. In their study, liveweights at 5 months postpartum ranged from 26.4 kg in two years old does to 30.76 kg in 6 years and older does. Similarly, Wilson et al. (1983) reported postpartum weights in Maasai SEA goat flocks ranging from only 23.4 kg in first breeders to 28.9 kg in fourth parity dams.

Relative liveweight increases during gestation were not generally larger in twin than in single carrying dams. Such a trend could only be detected in second and third parity does. The assumption is made that nulliparous and old animals (at least three prior kiddings) were less able to withstand the increased physiological stress associated with carrying twin fetuses to term, and therefore exhibited a slower rate of liveweight gain than their contemporaries carrying a single kid. In addition, the observed pattern may also be the expression of a reduced rate of body weight recovery following periods of nutritional stress, or of a lower rate of accumulation of body reserves during pregnancy. Within parity classes, the differences in liveweight due to litter size are most evident when comparing weight estimates obtained for week 20 of the reproductive cycle, i.e., just prior to parturition. For nulliparous and old does, no difference in body weights due to litter size was apparent, while for parities 2 and 3 twin carrying does were significantly heavier than those carrying a single kid. Similarly, mobilization of body reserves during the early stages of lactation appeared to be much more pronounced in the former than in the latter.

Effects of mating season

The different patterns of nutritional conditions engendered by the mating season treatment produced marked differences in liveweight changes and weight development curves in does over a reproductive cycle of one year duration. With respect to liveweight development during gestation, does were clearly advantaged when they were mated just prior to the long rainy season (mating season 1). Both liveweight at mating and at the prepartum measurement period were found to be heaviest in this group (35.4 and 42.0 kg, respectively). On the other hand, the largest relative liveweight gains of 32.2 and 37.8 percent in relation to liveweight at conception were achieved by does mated from October to January (mating season 5 and 6, respectively). A large part of these weight gains went into the replenishment of body reserves that were depleted during the preceeding long dry season.

When considering relative liveweight changes, net liveweight increases over the gestation period can be assumed to have occurred at least in those groups for which markedly positive relative liveweight changes were estimated until the postpartum measurement time point. This was the case in mating season groups 1, 4, 5, and 6 in which dams were, on average, heavier by 10, 13, 22, and 25 percent, respectively, at synchronized week 22 than at conception time. In a study on Scottish Half-Bred and Dorset Horn ewes, Treacher (1970) reported that in order to prevent utilization of fat reserves, relative liveweight gains of about 20 and 22 percent were required during late pregnancy. Over the last eight weeks of gestation, gains of this magnitude could not be observed in the present study. Thus, the estimates obtained from this data suggest that, to a large extent, increases in dam liveweight during gestation could be attributed to the growth of conceptus and/or the replenishment of body reserves. In contrast, nutritional stress during late pregnancy apparently had an adverse effect on dam liveweights in mating season groups 2 and 3. The respective liveweight development curves showed that goats had begun to lose weight from about 6 weeks prepartum onwards; this was undoubtedly related to the deficiency in the quality and quantity of feed resources at the peak and toward the end of the long dry season.

Consistent with expectations, the increased nutrient requirements at the onset of lactation generally could not be covered by available feed resources, so that this stage of the reproductive cycle was accompanied by massive mobilization of body reserves. Losses in body weight were especially drastic in females which gave birth at the start and at the middle of the long dry season (groups 1 and 2). In the latter groups, the peaks in average body weight losses relative to postpartum weight (18.4 and 11.8 percent in groups 1 and 2, respectively) were comparable to that observed by Mbayahaga et al. (1998) in a local Burundian strain of SEA goats after parturition in the dry season (11.1 percent). The fastest rate of recovery was observed in mating season 3, in which dams began to gain weight as soon as 5 weeks postpartum, in response to improving nutritional conditions at the onset of the short rainy season. At the other extreme, females which

gave birth at the beginning of the long dry season (mating season 1) were severely affected by the nutritional restriction experienced during the first four months of lactation, and these animals continued to lose weight until pasture forage production had improved in response to the onset of the short rainy season. Overall, liveweight development patterns during lactation were very different from those described previously for an extensive goat husbandry system operating under Mediterranean climate (Zygoyiannis and Katsaounis, 1986). The evidence presented in the latter study showed a steady increase in both liveweight and body condition score immediately after parturition and throughout lactation. The authors concluded that the available nutrition was at least adequate for the requirements of the indigenous breed studied. In the present setting, however, apparently in none of the mating season groups was the nutritional environment such that goats could display similar patterns of liveweight recovery after parturition. On the other hand, Gall (1980) supports the view that substantial mobilization of body fat stores at the beginning of lactation is a phenomenon particularly marked in goats due to their high initial milk production, for which the required dietary energy cannot be ingested by the animals even when fed on concentrates.

Under similar climatic conditions in Mali, Wilson and Light (1986) found that birth in the post-rain period and during the long dry season immediately following it had a negative impact on the reproductive potential of West African Sahel goats. The authors argued that due to poor nutrition such females took a longer time to return to breeding status, while does that kidded in the short rainy season recovered at a much faster rate due to the better forage availability. The present data, however, did not reveal comparable effects of liveweight development of does on their reproductive performance. In spite of the fact that animals allocated to mating season 1 lost, on average, about 17 percent of their body weight over the period from parturition to 22 weeks of lactation, no adverse effects on subsequent fecundity rates could be detected. During the last 10 weeks of the reproductive cycle relative liveweight gains of about 18 percent were achieved and does were estimated to recover at a rate roughly proportional to their weight at conception time. Similarly, the rapid decline in liveweight toward the end of the reproductive cycle observed in mating season 6 (-17 percent) apparently did not affect reproductive performance of does.

4.5 Conclusions

Seasonal breeding does not appear to confer any major advantage in terms of liveweight production of youngstock, except for the fact that mating during the short dry season from December to January should perhaps be avoided in order not to compromise liveweight development of kids. Wilson et al. (1984) arrived at similar conclusions in studying the effects of season of birth on liveweight development of kids in Maasai SEA goat herds. They found no significant differences weights of 18 months old kids and concluded that there would be little to be gained in terms of growth performance from attempting to control breeding. Nonetheless, birth weight and liveweight development of kids during the preweaning period are factors which can be expected to influence overall herd productivity through their effect on survivability. Indeed, as revealed by the present data, both survivability until weaning and weaning weights were highest when kids were born over the period from October to April (mating seasons 3 to 5).

Although body weight development profiles of does were seemingly dissimilar contrasted across mating season groups, this did not result in significant differences in estimated body weights of does at the end of the reproductive cycle, as long as goats were joined over the period from February to November (mating seasons 1 to 5). It is also worthwhile to note that within the latter groups there was virtually no difference in estimated weight at conception time and at 52 weeks after adjustment was made for the effect of parity. Mating in December and January (mating season 6), however, clearly resulted in markedly lower liveweights at the beginning and end of the reproductive cycle. In terms of balancing nutrient requirements of the dam and nutrient supply from pastures, this breeding period can be considered the least favourable among those considered in the present experiment.

Chapter 5

The impact of controlled breeding on milk production in pastoral goats in northern Kenya: an application of polynomial growth curve fitting

5.1 Introduction

Milk from cattle, camels, and, to a lesser extent sheep and goats is one of the most important products of pastoral production in semi-arid northern Kenya. Goats are kept primarily for subsistence meat production and for market sales or exchange of live animals. Although its contribution to overall consumption in pastoral households is limited, milk from goats is generally highly valued (McCabe, 1987). Goats confer an advantage in terms of food security since their drought mortality rates are lower compared to cattle, and their post-drought herd recovery rate is much faster than for cattle and camels. Due to their short gestation period, goats usually are the first animals to produce milk after a dry year or a drought period. They may as well play a critical role in balancing year-round supply with milk for subsistence due to their ability to lactate during dry seasons, when, for instance, cattle produce little or no milk at all (Schwartz & Schwartz, 1985; Grandin et al., 1991). The influence exerted by maternal milk yield on survival and growth of goat kids would seem to be of equal importance. Previous analyses in this series (Chapters 3 and 4) have shown that the total amount of milk available to kids until weaning is a critical risk factor affecting kid survival and has a strong impact on their growth performance. Hence, milk production can be assumed to make a significant contribution to overall biological productivity of goat herds and, ultimately, to the benefits derived from pastoral goatkeeping.

Traditional pastoral grazing systems have always had to cope with the effects of environmental seasonality on the achievement of their goals. This is clearly reflected by their management methods which involve flexible slaughter dates and stocking rates, herd mobility, as well as species mix. However, patterns of pastoral land use have changed considerably throughout semi-arid areas of Kenya due to the simultaneous pressure applied by several different factors on these systems, including human demographic factors and the commercialisation of pastoral production (Fratkin, 1992; Sikina et al., 1993; Schwartz et al., 1995; Roth, 1996). One of the central problems confronting pastoral producers in Northern Kenya today is the reduction in the mobility of their households and herds. The strategy of mobility is probably one of the most adapted means of overcoming the seasonal variation in pasture resources (Niamir, 1990). Alternatives to herd mobility as an efficient strategy to reduce the impact of seasonal nutritional deficits on livestock production are few. One possibility is to manipulate the total seasonal nutrient requirements of the herd, instead of attempting to improve the supply side of the nutrient balance. This could for instance be accomplished by limiting reproduction to a short time period in a year, so as to synchronize reproductive stages of high nutrient requirements with pasture forage production. The present chapter investigates the effect of such a controlled seasonal breeding strategy on milk production in a herd of Small East African (SEA) goats.

The analysis is based on fitting polynomial growth curve models to both daily and cumulative milk yield data obtained from an experiment conducted under simulated pastoral herd management in Isiolo District, Northern Kenya. Part of these data have been analysed previously using a different methodology and to address different objectives. Using the incomplete gamma function (Wood, 1967), the study of Wahome et al. (1994) focused on characterising the general shape of the lactation curve and the main factors that influence milk production levels in SEA goats under pastoral management. Although it is the most widely used functional form for modelling lactation curves for domestic livestock, the incomplete gamma function has a number of well known limitations, including overprediction of daily milk yield at the beginning of lactation, underestimation of peak daily milk yields, and failure to account for autocorrelated error terms (Pérochon et al., 1996; Scott et al., 1996). That the incomplete gamma function does not account for the correlation between repeated measurements on the same animal is likely to invalidate the analysis of functional parameters and inferences concerning the effect of treatment and/or classification factors on the shape of the lactation curve. Moreover, the incomplete gamma function is a rather inflexible method for describing the evolution of daily milk yields over time. It is generally incapable of dealing with major alterations in milk yield induced by such events and effects as fluctuations in nutrient supply and season of kidding. However, under semi-arid rangeland conditions, milk production is more a function of season or

nutrient availability than stage of lactation (Nicholson, 1984). Hence, both individual animal and seasonal variation cause estimates to have large standard errors. Multiple peaks can be expected to arise in lactation curves in response to changing nutritional conditions, but are normally considered to be aberrant and are often omitted from consideration when fitting the incomplete gamma function to lactation data (e.g., Pérochon et al., 1996). In contrast, fitting polynomial growth curves to longitudinal lactation data using the general linear mixed model framework (Laird & Ware, 1982) is a particularly flexible method for simultaneously accommodating variability due to the environment, individual animal differences, and dependent error terms.

5.2 Materials and Methods

Experimental data

Data were from an experiment in which milk production was recorded in several seasonal breeding groups of SEA goats maintained at the Ngare Ndare Research Station of the University of Nairobi in Isiolo District, northern Kenya. Details of the experiment with regard to herd management and data recording were described before in Chapters 2 and 3. In short, breeding groups of 18 does each, with a balanced age and weight structure, were established. The experiment was initiated at the end of January 1984, when a buck was introduced into the first breeding group for two months. The buck was transferred afterwards to consecutive groups for the same duration, so as to achieve year-round mating, kidding, and weaning. Mating in the last breeding group (number 18) started at the end of March in 1987. Kids were weaned at an age of 16 weeks. Prior to analysis, data from the individual breeding groups were grouped into six different mating seasons. Three complete production cycles years were obtained for five of these six consecutive two month mating seasons. The sixth season had only two complete cycles, because data from the last breeding group (number 18) had to be discarded due to incomplete records. The experimental treatment thus consisted of six mating seasons, the first one, labelled as mating season 1, ranged from February to March, and the last one, labelled as mating season 6, ranged from December to January. Mating seasons 4 and 5 (August to October, and October to December, respectively) had to be assumed to have taken place over a period of three months due to a delay of one month which occurred in setting up the first breeding group of mating season 4 in 1984.

Time in the experiment was divided into periods of two weeks, each period starting and ending on a Monday. Routine measurements of weight (kg) of all animals and milk production of dams were carried out at the beginning of each two-week period. Adult animals were weighed using a weighing crate and measurements were made to the nearest 0.5 kg. Handmilking was done on two consecutive days of each fortnightly period with the kid close by, except for does whose kids died, which were milked daily. On the first day, the right half of the udder was milked in the evening and the following morning. The left half of the udder was similarly milked on the second day. Kids were not allowed to suckle during the night preceding the morning milking. The total volume of milk collected on the two consecutive days was taken as the average daily yield of the doe for the current period.

Pasture condition was judged during every recording period using a subjective phenological pasture condition score using score values from 1 to 4 according to greenness and abundance of the herblayer (range condition score [I]). Scores of 1 to 2 generally occurred during the dry seasons, and 3 and 4 during and immediately after the rainy seasons. The contribution of bushes, trees, and of high quality litter such as leaves, flowers and fruits to diet of goats was taken into account by upgrading the herblayer condition score to a maximum value of 5 (range condition score [II]).

Traits studied

Lactation curves (average daily milk yield (g)) and cumulative milk yield (kg) curves were estimated from the series of biweekly milk yield measurements obtained from the experiment, ranging from the postpartum recording date to the 28th week of lactation. The average daily milk yield of each doe for each two week period was assumed to be equivalent to the total volume of milk collected at the recording date. Total milk yield for each period was then calculated as the sum of the product of the measured daily milk yield and the length of the time interval (14 days). Observations pertaining to does which entered a new reproductive cycle or were found to be pregnant before the end of the current lactation were discarded from the data set.

Statistical analysis

The general linear mixed model framework, as implemented in the SAS procedure MIXED (SAS Release 6.12, 1996), was used fit polynomial growth curve models to daily and cumulative milk yield data. The aim

was to characterize the evolution of daily and total yield curves over time for subjects in the six different mating season groups, and to investigate the effects of other covariates on the shape of these curves. In this respect, approximating the actual functional form of response curves through a natural polynomial in time was found to be particularly useful, since this method allows the estimating of separate polynomial growth curves for each treatment and/or classification factor level, which then could be used to compare performances at different time points (Rowell & Walters, 1976; Cullis & McGilchrist, 1990; Jones, 1993; Diggle et al., 1994; Cnaan et al., 1996).

The general form of the linear mixed models used to model milk production over time is as follows. According to Laird and Ware (1982), a general linear mixed model for longitudinal data with a sequence of p measurements on subject i can be specified as

$$y_i = \mathbf{X}_i\beta + \mathbf{Z}_i\gamma_i + \varepsilon_i, \qquad (1)$$

where

y_i = a $p_i \times 1$ vector of the response variable for subject i
$\mathbf{X}_i$ = a known $p_i \times q$ design matrix
β = an unknown $q \times 1$ vector of fixed effects coefficients
$\mathbf{Z}_i$ = a known $p_i \times r$ design matrix
γ_i = an unknown $r \times 1$ vector of random subject coefficients, assumed to be independently distributed across subjects with distribution $\gamma_i \sim N(0, \sigma^2\mathbf{B})$, where $\mathbf{B}$ is the between subjects covariance matrix
ε_i = a $p_i \times 1$ vector of within subjects errors assumed to be distributed as $\varepsilon_i \sim N(0, \sigma^2\mathbf{W}_i)$, where $\mathbf{W}_i$ is the within subjects covariance matrix

The columns of the model matrices $\mathbf{X}_i$ and $\mathbf{Z}_i$ consist of indicator variables corresponding to the levels of the fixed and random subject effects, respectively. Note that the fixed-effect part of model (1) can incorporate polynomial time trends, treatment and/or classification factor effects and their interactions with polynomial terms, as well as time-changing covariates such as range condition scores (Cnaan et al., 1996). In its most general form, the specification of the random effects through the design matrix $\mathbf{Z}_i$ can be entirely independent of that of the fixed effects design matrix $\mathbf{X}_i$, but often is assumed to be a subset of $\mathbf{X}_i$. In longitudinal studies, these between subject components of variance are used to model the random deviations of the intercept and possibly higher degree polynomial powers of the time of observation for subject i from the subject's group mean intercept and higher degree polynomial time trends (Jones, 1993; Cnaan et al., 1996).

The linear mixed model formulation is very general since different subjects can have different numbers of observations as well as different numbers of observation times. Therefore, subjects with incomplete data do not need to be discarded from the analysis. Equation (1) can further be expanded to incorporate additional random effects by defining a $p_i \times v$ design matrix, $\mathbf{U}_i$, of random effects and a corresponding unknown $v \times 1$ vector, τ_i, of random effects coefficients:

$$y_i = \mathbf{X}_i\beta + \mathbf{Z}_i\gamma_i + \mathbf{U}_i\tau_i + \varepsilon_i. \qquad (2)$$

The random effects, τ_i, are assumed to be identically and independently distributed as $\tau_i \sim N(0, \sigma^2\mathbf{I})$, where $\mathbf{I}$ denotes the $p \times p$ identity matrix. In the present study, the effect of production cycle (three levels) and its interaction with the mating season treatment were considered as such random effects and included in all preliminary models fitted to the data. Model construction and data analysis encompassed the same steps as those described previously in Chapter 4. Using plots of individual and group mean profiles as a starting point to obtain a visual picture of possible models for the data, various models that included random subject effects, serial correlation, and both random subject effects and serial correlation were computed. In addition, one model with and one without random subject effects were fitted to the data using an unstructured covariance matrix. Akaike's Information Criterion (AIC) was used a decision criterion for final model selection. The serial correlation structure employed was a heterogeneous first-order autoregressive structure (ARH[1] in the SAS PROC MIXED terminology).

Table 5.1 summarizes the predictor variables included in preliminary analyses. Selection of suitable final models was based upon fitting successive nested model versions, and omitting variables from the linear

Table 5.1. Explanatory variables included in initial models fitted to lactation data. Nesting factors are given in square brackets. (PC=production cycle; MS=mating season).

Random effects	Fixed effects
• dam [PC×MS] • production cycle {1; 2; 3}	• mating season (1 to 6) • parity at breeding (0; 1; 2; ≥3) • weight at breeding in kg (< 25; 25 to 30; 30 to 35; 35 to 40; ≥40) • type of birth (single; twins) • Lagged median range condition score [I] and [II] for the current and the two immediately preceeding periods (integer scores of 1 to 4, and 1 to 5, respectively) • time

predictor when the likelihood ratio (LR) statistic indicated that the model including an additional parameter did not fit significantly better than the simpler model. Fixed-effects terms and interactions among fixed-effects were excluded from the model when the probability of obtaining a greater χ^2-value than the observed LR test statistic from a χ^2 distribution with r degrees of freedom was greater than 0.15, r denoting the additional parameters that have to be estimated in the larger of the two models. The same procedure was applied to test for the significance of random effects, except that the p-value for the LR statistic was obtained by taking half of the probability of a greater χ^2 from a χ^2 distribution with one degree of freedom, given that only a one-sided test is needed in this case and only one additional parameter is estimated upon including a random effect into the model. Orthogonal polynomials were used instead of natural polynomials to model time trends in order to avoid problems caused by multicollinearity between polynomial powers of the time of observation (Steel and Torrie, 1980; Draper & Smith, 1981).

In order to avoid bias in estimated fixed effect coefficients due to multicollinearity in the linear predictor, the effects of postpartum live weight, litter size, and range condition scores [I] & [II] on response patterns were studied separately from those of mating season and parity. The assumptions of normality and homogeneity of variances across the cells of the between-groups design were tested using the Kolmogorov-Smirnov One Sample Test and the Bartlett-chi-square test, respectively. Graphical inspection was used to assess the correlation of mean response values with the variability (standard deviations and variances) across the cells of the design. In cases where the data did not fulfil one of the foregoing assumptions, the Box-Cox procedure as described by Neter et al. (1996) was applied to identify an appropriate transformation of the continuous response variable from the family of power transformations. When making multiple comparisons of factor level means, the experimentwise error rate was controlled at the prespecified level of α=0.05 by using both the Bonferroni and Tukey multiple comparison procedures. The procedure giving the narrower confidence limits was then chosen to report significance probabilities of differences in factor level means (Neter et al., 1996). Tests of hypotheses concerning specific linear combinations of parameter estimates were obtained by specifying appropriate *estimate* and *contrast* statements in the SAS procedure MIXED.

5.3 Results

Lactation curves

Summary information on the models fitted to daily milk yield data appear in Table 5.2. Mean response values were found to be highly correlated with the variability across cells of the design at each follow-up time point, so a square root transformation of milk yield data was used to stabilize variances. Lagged range condition score [I] was not significant in any of the models fitted to the data. In both final models the general level of estimated response profiles varied quite substantially between individual dams, that is, some were intrinsically high yielders, others low yielders. The importance of this stochastic variation is indicated by the numerical magnitude of the highly significant dam variance component (p< 0.001 in both models) in Table 5.2, whose realized value represents a random intercept, i.e. the amount by which all measurements on the same experimental unit are raised or lowered relative to the population average.

Table 5.2. Tests of fixed effects and estimates of variance components and covariance parameters for lactation curves fitted to daily milk yields (square root-scale) by a) mating season and parity class, and b) litter size, postpartum liveweight, and lagged range condition score [II].

	a)				*b)*			
*Fixed effects**)	*df*	χ^2	$p>\chi^2$		*Fixed effects*	*df*	χ^2	$p>\chi^2$
MS	5	9.8	0.081		Litter size	1	6.2	0.013
Parity	3	4.3	0.232		P.p.weight	3	19.3	< 0.001
t	1	881.9	< 0.001		RC[II]	4	385.0	< 0.001
t^2	1	4.9	0.027		t	1	730.6	< 0.001
t^3	1	6.9	0.009		t^2	1	0.2	0.643
t^4	1	27.0	< 0.001		t^3	1	6.0	0.014
t×MS	5	296.0	< 0.001		t^4	1	15.8	< 0.001
t^2×MS	5	89.4	< 0.001		t×litter size	1	4.4	0.037
t^3×MS	5	52.8	< 0.001		t×p.p.weight	3	14.2	0.003
t^4×MS	5	52.7	< 0.001		t×RC[II]	4	7.5	0.112
	t×RC[II]	4	7.5	0.112				

*Covariance parameters***)	*time (weeks)*	*estimate*	*std. error*	*Covariance parameters*	*time (weeks)*	*estimate*	*std. error*
ρ		0.55	0.02	ρ		0.58	0.02
σ^2	2	17.5	1.63	σ^2	2	18.1	1.70
	4	13.6	1.25		4	15.8	1.45
	6	15.3	1.40		6	16.2	1.50
	8	15.8	1.44		8	19.1	1.73
	10	12.4	1.17		10	12.5	1.20
	12	11.0	1.05		12	11.3	1.09
	14	11.3	1.07		14	11.7	1.12
	16	10.9	1.04		16	12.0	1.14
	18	8.6	0.86		18	9.3	0.94
	20	10.2	0.99		20	10.8	1.07
	22	12.9	1.25		22	14.5	1.40
	24	11.1	1.11		24	12.2	1.22
	26	8.6	0.91		26	10.5	1.10
	28	11.3	1.24		28	12.3	1.37

Variance components			*Variance components*		
$\sigma^2_{dam[PC\times MS]}$	8.5	1.10	$\sigma^2_{dam[PC\times MS]}$	10.6	1.30
$\sigma^2_{PC\times MS}$	4.7	1.63	σ^2_{PC}	1.0	0.85

*) MS=mating season.

**) ρ=autoregressive parameter standing for the correlation between adjacent observations on the same subject; σ^2=variance of an observation at a given time point; PC=production cycle. Note that standard errors for variance components are based on asymptotic normality.

Two additional results to note are that average yield levels in each mating season treatment group differed considerably between replications of the experiment ($\sigma^2_{PC\times MS}$=4.7, p< 0.01), whereas the expected variation between production cycles only, irrespective of mating season, was much smaller, though still statistically significant (σ^2_{PC}=1.0, p< 0.05).

From the response profiles depicted in Figure 5.1 it is apparent that milk yields in the first two weeks of lactation where negatively affected (< 400g·day^{-1}) when kidding took place between June and September (mating season groups 1 and 2), whereas maximum initial yields of about 450 to 550 g·day^{-1} were achieved at the onset and during the long rainy season (groups 5 and 6). The characteristic peak in milk yield curves usually observable after 4 to 6 weeks of lactation appeared only when does had access to adequate forage supply. This was the case for goats in group 3 during the short rains with a peak yield of 428g·day^{-1}, and for

those in groups 5 and 6 during the long rains, which produced maximum yields of 532 and 580g·day^{-1}, respectively. Milk yields in groups 1 and 2 were significantly lower ($p< 0.05$) than those achieved in groups 5 and 6 in lactation weeks four to eight.

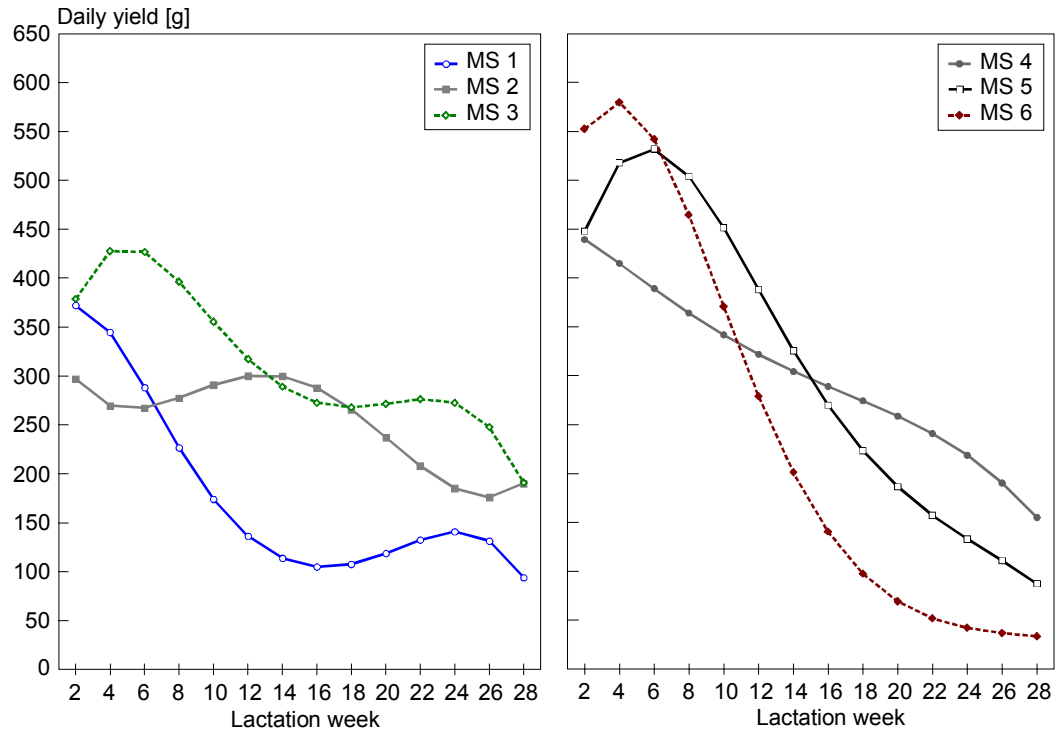

Figure 5.1. Estimated lactation curves (least squares means) by mating season (MS).

The most rapid decline in milk production rates early in lactation were observed at the onset of the long dry season in mating season groups 1 and 6. By 12 weeks, yields in group 1 were significantly lower than in all other group ($p< 0.05$), but recovered slightly from a low level of 105g·day at weaning to a local maximum value of 115g·day^{-1} around 24 weeks in response to improving feeding conditions during the short rains. In contrast, lactating does in group 6 rapidly dried off during the course of the long dry season and yields dropped below 100g·day^{-1} shortly after weaning. Although lowest in the first two weeks of lactation, yields in group 2 never fell much below 300g·day^{-1} until weaning, and started to decline gradually thereafter. The goats in this group produced their maximum milk yield at 14 weeks during the short rains. In group 3, milk production rates decreased slowly until weaning and plateaued at about 270g·day^{-1} up to 24 weeks. The pronounced responses to changing environmental conditions observable in the lactation curves of the first three treatment groups were absent in that for group 4. Here, milk yields declined almost linearly from parturition until the end of follow-up. Does kidded at the onset of the long rains in group 5 also showed continuously declining milk production rates following the peak in the sixth week of lactation.

Polynomial contrasts revealed a significant quadratic trend ($p< 0.05$) in average daily milk yields with increasing parity stage from parturition until 20 weeks of lactation. Thereafter, no systematic trend across parity levels could be detected. In the first two weeks of lactation, milk production rates ranged from 390g·day^{-1} in the first lactation to 455g·day^{-1} in the fourth or later lactations. Peak milk production was attained between the second and fourth lactation week and declined gradually thereafter until the end of the follow-up period. The highest level of production was observed in the third parity, although it did not differ significantly from that achieved in the second parity and was barely discernible from the latter after three months of lactation. Until 10 weeks, the lowest yields were produced by first lactating does, but thereafter these showed a greater persistence and produced increasingly more milk per day than does in their fourth or later lactation. Over the entire observation period, all pairwise comparisons of milk yields across parity levels failed to reach significance.

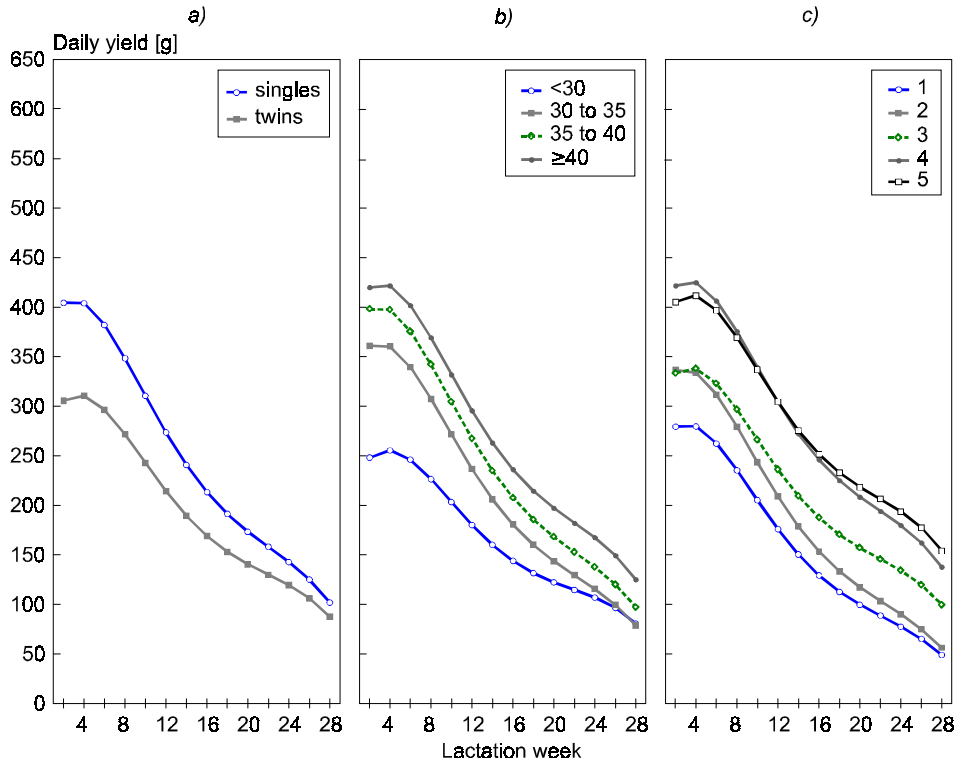

Figure 5.2. Estimated lactation curves (least squares means) by *a)* litter size, *b)* postpartum live weight (kg), and *c)* lagged range condition score [II] in each time interval.

Litter size markedly affected milk production levels (Figure 5.2*a*). Yields in does nursing twins were significantly lower than in those nursing a single kid until the 24th lactation week ($p< 0.01$). The latter produced 98g·day^{-1} or 32 percent more milk in the first two weeks of lactation. This difference in yields reduced to 14g·day^{-1} or 16 percent until the end of follow-up at 28 weeks. A clear differential effect on milk production rates was also exerted by postpartum live weight state of does (Figure 5.2*b*). As expected, milk yield level was a linear function of postpartum live weight ($p< 0.001$) at each measurement time. During the first two weeks of lactation, the lightest does produced approximately 41 percent less milk than the heaviest ones ($p< 0.001$). This difference decreased only slightly up to weaning (39 percent) and 28 weeks of lactation (36 percent), and remained significant until 24 weeks. Up to 12 weeks, significant differences ($p< 0.05$) in daily milk yields could only be detected between the lightest goats and those weighing more than 30 kg postpartum. Does heavier than 35 kg after parturition continued to produce significantly more milk until 18 weeks of lactation than those weighing less than 30 kg. At later stages up to 24 weeks of lactation, the only significant difference observed was that between the lightest and heaviest animals.

Differential effects of lagged range condition scores [II] in each follow-up time interval on milk production rates were substantial, as may be seen from the response profiles depicted in Figure 5.2*c*. Not surprisingly, milk yields in each time interval were found to be an increasing function of range condition. This trend was fairly consistent over the entire observation period, although crisscrossing of lactation curves of scores 4 and 5 occurred around weaning time. The difference in average yields during the first two weeks of lactation between scores 1 and 4 and 5 amounted to 143 and 126 g·day^{-1} (+51 and +45 percent), respectively. By the end of the observation period, this discrepancy had decreased in absolute terms to respectively 89 and 105 g·day^{-1}. Both differences, as well as that between score 1 and 3 were significant throughout the observation period ($p< 0.01$). Milk yields under intermediate forage conditions of 2 and 3 were also significantly lower at all observations times than under scores of 4 and 5 ($p< 0.01$).

Table 5.3. Tests of fixed effects and estimates of variance components and covariance parameters for growth curves fitted to cumulative milk yields (square root-scale) by *a)* mating season, and *b)* litter size and postpartum live weight.

	a)				*b)*		
*Fixed effects**)	*df*	χ^2	$p>\chi^2$	*Fixed effects*	*df*	χ^2	$p>\chi^2$
MS	5	20.4	0.001	Litter size	1	10.5	< 0.001
t	1	3430.4	< 0.001	P.p.weight	3	28.1	< 0.001
t^2	1	1098.4	< 0.001	t	1	2253.9	< 0.001
t^3	1	338.2	< 0.001	t^2	1	754.6	< 0.001
t^4	1	85.3	< 0.001	t^3	1	238.7	< 0.001
t×MS	5	120.6	< 0.001	t^4	1	72.4	< 0.001
t^2×MS	5	110.6	< 0.001	t×litter size	1	2.7	0.102
t^3×MS	5	118.8	< 0.001	t^2×litter size	1	2.4	0.123
t^4×MS	5	107.5	< 0.001	t×p.p.weight	3	10.2	0.017
				t^2×p.p.weight	3	23.2	< 0.001
*Covariance parameters***)	*time (weeks)*	*estimate*	*std. error*	*Covariance parameters*	*time (weeks)*	*estimate*	*std. error*
ρ		0.982	0.003	ρ		0.964	0.008
σ^2	4	0.123	0.048	σ^2	4	0.064	0.042
	8	0.517	0.101		8	0.407	0.098
	12	0.705	0.119		12	0.521	0.104
	16	0.702	0.117		16	0.421	0.084
	20	0.636	0.109		20	0.294	0.062
	24	0.538	0.099		24	0.157	0.042
	28	0.458	0.095		28	0.065	0.029
Variance components				*Variance components*			
σ^2dam[PC×MS]		0.672	0.071	σ^2dam[PC×MS]		0.975	0.093
σ^2t×dam[PC×MS]		0.021	0.002	σ^2t×dam[PC×MS]		0.038	0.004
σ^2PC×MS		0.185	0.071	σ^2PC		0.073	0.061

*) MS=mating season.

**) ρ=autoregressive parameter standing for the correlation between adjacent observations on the same subject; σ^2=variance of an observation at a given time point; PC=production cycle. Note that standard errors for variance components are based on asymptotic normality.

Cumulative milk yields

Cumulative milk yield data were transformed to the square root scale prior to model fitting in order to correct for correlated means and variances across cells of the design at each measurement time. In contrast to the analysis of daily milk yields, in all preliminary models fitted, patterns of cumulative milk yield over time did not differ significantly between parity stages. This was in accordance with the findings of the analysis of daily milk yields reported above that revealed no significant differences across parity stages at individual observation time points, despite the fact that some discrepancies in the shape of the corresponding lactation curves had been detected. Cumulative milk yields were finally assessed in terms of mating season, litter size, and postpartum live weight of does (Table 5.3). The latter two effects were, again, analysed separately since they were confounded with the mating season treatment effect.

As may be seen from the statistical results presented in Table 5.3, a very large between-animal variation in total milk yields was present in both models fitted. Due to the interaction of the random doe effect with the linear slope, individual response profiles did not only differ in their general level, but also in shape. The intercepts of mating season group response profiles were also not constant across production cycles, as indicated by the relatively large production cycle×mating season variance component. In comparison, the

variation in the general level of response profiles due to the production cycle random effect itself was much smaller, though still significant at the five percent level.

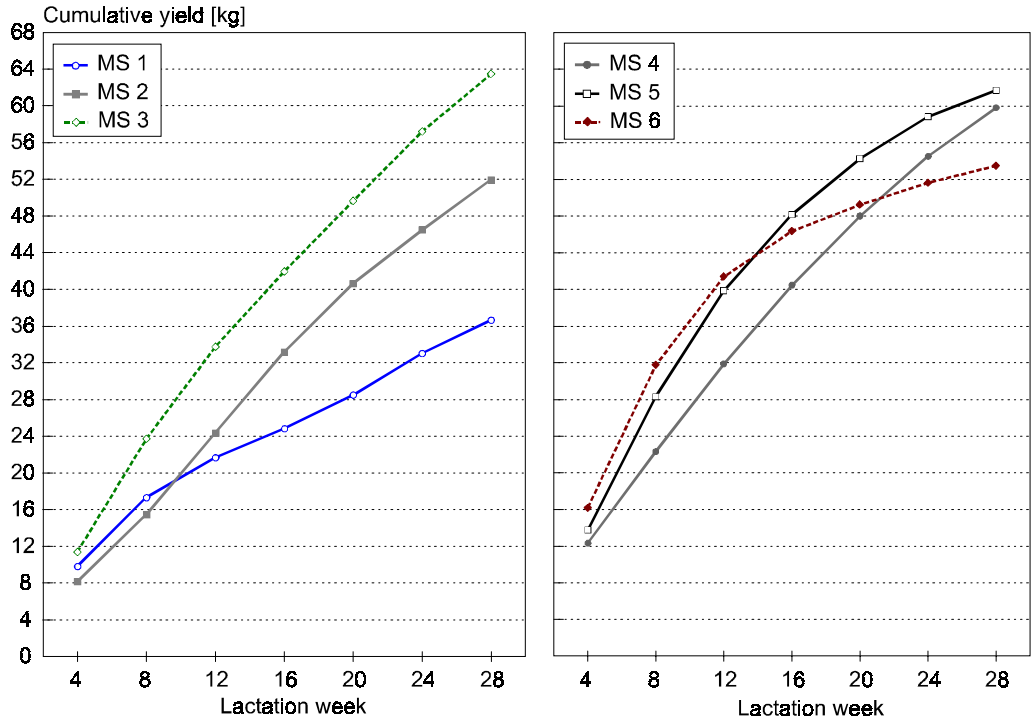

Figure 5.3. Estimated cumulative milk yield curves (least squares means) by mating season (MS).

Total milk produced by mating season after 4 weeks of lactation ranged from 8.3 kg in group 2 to 16.2 kg in group 6 (Figure 5.3 and Table 5.4). The highest yield until weaning time, however, was achieved in group 5 with 48.2 kg, followed by group 6 with 46.4 kg. Intermediate levels of production of slightly more than 40 kg were predicted for groups 3 and 4. Nutritional constraints experienced during the long dry season clearly had a detrimental effect on response patterns in the first two mating season groups, although after weaning this trend was attenuated to some extent in group 2 by a rise in milk yields during the short rainy season. Cumulative yields at 28 weeks of lactation were lowest in group 1 with an average of only 36.6 kg milk per doe, approximately 42 percent less than in group 3 which displayed the best lactation performance. Average production levels in groups 4 and 5 were only slightly lower than in the latter. Although not statistically significant, total milk production until 28 weeks of lactation was markedly lower in groups 2 and 6, amounting to 52 and 53.2 kg milk, respectively. Throughout the observation period, significant differences could only be detected between mating season groups 1 and 3 to 5 from 8 weeks onwards, and between groups 1 and 6 from 8 to 24 weeks of lactation.

Total milk production in does nurturing twins was significantly lower at all stages than in does nurturing a single kid (Table 5.4). By 4 weeks, the former had produced about 22 percent less milk than the latter. The relative difference in total yields diminished slightly during later stages and amounted to 19 percent at 28 weeks of lactation. Total milk yields across postpartum live weight classes (Table 5.4) followed the expected course, with a significant linear trend at all stages with increasing live weight of does after birth ($p < 0.01$). The mean total yield predicted for the lightest group was only 70, 65, and 67 percent of that predicted for the heaviest group at 4, 16, and 28 weeks of lactation, respectively.

Table 5.4. Least-squares means and 95 percent confidence limits (in brackets) of cumulative milk yields at selected time points during lactation, according to mating season, litter size and postpartum live weight of does.

Term		time in weeks*) 4	16	28
Mating season	1	9.8	24.8^{a}	36.6^{A}
		[6.5; 13.9]	[19.0; 31.4]	[29.5; 44.5]
	2	8.2	33.2	52.0
		[5.1; 12.0]	[26.2; 41.1]	[43.1; 61.7]
	3	11.4	41.9^{b}	63.4^{B}
		[7.6; 15.9]	[33.9; 50.8]	[53.6; 74.2]
	4	12.3	40.4^{b}	59.8^{B}
		[8.5; 17.0]	[32.8; 48.9]	[50.4; 70.0]
	5	13.8	48.2^{b}	61.7^{B}
		[9.5; 18.8]	[39.3; 57.9]	[51.7; 72.6]
	6	16.2	46.4^{b}	53.5
		[10.8; 22.7]	[36.4; 57.5]	[42.8; 65.3]
Litter size	single	12.1^{a}	39.9^{A}	56.8^{A}
		[9.4; 15.1]	[35.0; 45.2]	[50.8; 63.1]
	twins	9.9^{b}	33.1^{B}	47.9^{B}
		[7.3; 12.9]	[28.3; 38.3]	[42.0; 54.2]
Postpartum	< 30	8.6^{a}	28.0^{A}	42.0^{A}
weight [kg]		[5.8; 11.8]	[23.0; 33.5]	[35.5; 49.0]
	30 to 35	10.7	35.7^{B}	50.0^{B}
		[8.0; 13.8]	[30.7; 41.2]	[43.8; 56.6]
	35 to 40	12.6^{b}	40.2^{B}	55.8^{BC}
		[9.6; 15.9]	[34.8; 45.9]	[49.3; 62.8]
	≥40	12.3	42.9^{B}	62.1^{C}
		[8.7; 16.5]	[36.1; 50.3]	[53.5; 71.4]

*) Factor level estimates at a given time point without common letters in their superscripts differed at the five percent (lower case letters) or one percent (upper case letters) level of significance.

5.4 Discussion

Using data from the same experiment, Wahome et al. (1994) have previously presented estimates of curves for daily milk production over a period of 31 weeks following kidding, according to vegetation condition around parturition time, year, dam parity, and litter size. As mentioned above, the analytical strategy adopted by these authors was to fit an incomplete gamma function to the test-day yield records of each animal on study using a nonlinear estimation procedure, and to subject the resultant estimates of functional parameters to an analysis of variance. Estimated least squares means of the functional parameters were subsequently employed in constructing lactation curves for each level of the predictor variables. Principally, this approach must be based upon a sample of equidistant and complete series of milk yield records taken at a common set of observation times up to a specified end-of-lactation-date in order to be technically feasible and to produce valid parameter estimates (Diggle et al., 1994). It follows that incomplete or truncated series, as well as series with missing records at individual test-days must either be deleted or, alternatively, a missing value imputation technique (which introduces substantial amounts of error) has to be applied to these data (see, for example, the study of Zoa-Mboé et al. (1996, 1997)). Similar considerations would need to be made when addressing the problem of irregularly spaced recording intervals, but this was not the case for the present data. Wahome et al. (1994), however, did not state how they dealt with missing and/or incomplete lactation data. In contrast, with the general linear mixed models employed in this study it is easy to handle missing values in the dependent variable since the subjects are allowed to have unequal numbers of repeated observations or to be measured at different occasions. To obtain valid and efficient estimates requires only

that the missingness itself not be related to the outcome (see Cnaan et al. (1997) for further details). Thus, difference in analytical approach alone could be expected to result in discrepancies between model predictions obtained in this work and those reported by Wahome et al. (1994). Moreover, the present analysis focused on the investigation of the effect of mating season on lactation performance, and used only 231 lactations observed during this particular experiment entered the statistical analysis, while Wahome et al. (1994) state that in their analysis records of 257 does were used to fit lactation curves (note that the latter figure differs from that given in the abstract of the same paper, i.e., 267 lactations). Obviously, they must have used records pertaining to animals maintained at the Ngare Ndare research station, but which did not participate in the restricted breeding experiment. In the following discussion, we highlight any major discrepancies between both sets of results whenever they occur.

Average daily milk production in this flock of SEA goats was within the range reported by Devendra and Burns (1983) for small-sized indigenous African breeds such as Maradi and West African Dwarf goats. Daily yields were also comparable to those obtained by Ruvuna et al. (1995) for SEA and Galla goats under more favourable environmental conditions in Western Kenya, and those reported by Blackburn and Field (1990) for the same breeds under arid conditions in Northern Kenya. For SEA goats, Ruvuna et al. (1995) give estimates of average initial and peak morning yields of 345 and 347 $g \cdot day^{-1}$, respectively, while the lactation curves presented by Blackburn and Field suggest average initial and peak yields during the wet season of about 400 and 550 $g \cdot day^{-1}$, and thus were similar to those estimated from the present data. Additionally, after adjusting for the effect of mating season or range condition, the shape of estimated lactation curves were similar to those reported from other studies, where an initial rise in yields up to the second to sixth week of lactation was followed by a steady decline in yields until the end of lactation (Ehoche and Buvanendran, 1983; Raats et al., 1982). However, the rapid fall in yields after weaning noted in several other studies (e.g., Morand-Fehr and Sauvant, 1980; Zygoyiannis and Katsaounis, 1986) and which was attributed to the removal of the suckling stimulus could not be detected.

Although comparative lactational performance is difficult to assess based on absolute figures, it is nevertheless clear that the average cumulative milk production until 12 weeks of lactation of 31.7 kg (95 percent confidence limits : [28.9; 34.7]) estimated in this experiment is low compared to the performance reported for other, larger sized African breeds such as, for example, Boer goats. Based on the average daily yields reported by Raats et al. (1983), Boer goats can be expected to produce between 123 and 207 kg over a lactation period of 12 weeks, depending on parity number and litter size. To some extent, this superiority in milk production is not surprising, since milk yield usually tends to be positively correlated with almost all body dimensions, including liveweight and udder volume (Devendra and Burns, 1983; Gall, 1980). Apart from differences due to adult size, however, the comparatively low milk yields in SEA goats are certainly also related to both the genetic potential of this breed as well as to the poor nutritional environment to which animals are exposed. For instance, the substantial effect of forage quality and quantity on offer on milk yield was demonstrated by the large deviation in average daily milk yield curves between range condition score levels. Also, the statistical analysis revealed a remarkable variation in the scale (intercept) as well as in the linear slope of cumulative milk production curves among does, even after adjustment was made for the random effect of production cycle and its interaction with mating season. This indicates considerable scope for selection on milk production within local herds of SEA goats. For selection purposes, total yield until 4 weeks of lactation appears to be a fairly good indicator of cumulative lactation performance. The growth curve model fitted to cumulative milk yields, adjusted for the effect of mating season, gave an estimated correlation between adjacent observations on the same animal of $\rho=0.98$, so that the correlation between total yields measured at the end of week 4 and 28 amounts to $\rho^6=0.90$.

Effect of litter size

Litter size had a substantial influence on lactation curve differences for both daily and cumulative yield traits. Does suckling twins produced on average about 32 and 16 percent less milk per day during the first and last two weeks of follow-up, respectively, than those suckling a single kid. Although it is well established that litter size can be an important source of variation affecting milk production in goats, the results reported in the literature would have suggested a relationship in the opposite direction. Almost all workers found that milk yields improved with litter size, and often this trend was attributed to the associated increase in suckling stimulus (e.g., Ehoche and Buvanendran, 1983; Mavrogenis et al., 1984; Raats et al., 1982; Skinner, 1972; Zygoyiannis and Katsaounis, 1986). Landau et al. (1996) point out that the number of fetuses also has a beneficial effect on mammary development in goats, which apparently is mediated through the activity of placental lactogen. On the other hand, both of these stimulating effects could be more than offset when animals are maintained under nutritional conditions promoting negative energy balances during late pregnancy. This interpretation seems to be supported by Sauvant et al. (1991), who argue that reduced milk production in twin nursing goats most likely results from ill-management of body reserves, and not from

deficient mammary development. Although reproducing animals are able to maintain high levels of milk production even under conditions of restricted feed supply by mobilizing body reserves, there are obviously limits to this so-called buffer-effect (Santucci et al., 1991). Upon examining body weight development patterns during pregnancy and early lactation, the present data revealed that at least in the first and fourth or greater parity does, relative body weight increases until parturition were lower, and mobilization of body reserves during the early stages of lactation appeared to be much more pronounced in animals carrying twins than in those carrying singles. However, this pattern was reversed for second and third kidding does, so that the increased physiological stress associated with carrying twin fetuses to term can only provide partial explanation for the observed negative trend in milk yields with increasing litter size.

Effect of dam parity

Although the effect of dam parity on milk yield in goats is well established, the present analysis failed to reveal clear-cut differences in terms of scale and shape of lactation curves with increasing number of kiddings. Only slight evidence for the effect of parity on the linear slope of curves for daily production was obtained ($p < 0.15$), while the curves for cumulative yield up to 28 weeks following freshening were not affected at all by this factor. As indicated by Devendra and Burns (1983), effects of parity as well as age on daily production may be difficult to detect due to the influence of various environmental and managemental factors. However, up to 20 weeks of lactation, initial and peak yields followed a quadratic trend with increasing parity. Maximum initial and peak daily yields were achieved by third parity dams. Overall, this trend in milk yield compares favourably with the results reported by other workers. For instance, Alpines, Saanens and Toggenburgs displayed increasing milk yields up to the third to fourth lactation (Kennedy et al., 1981); similar patterns were also described by Gipson and Grossman (1990) in their review on lactation curves in dairy goats. The main reason for the initial rise in milk production with advancing parity is that milk yield is proportional to the mammary alveolar surface area, which can be assumed to increase between successive lactations (Gall, 1980; Raats et al., 1982). Parity number also affected the persistency in milk yields. If persistency is defined as the average rate of decline in estimated daily milk production following peak yield (attained at 2-4 weeks of lactation for all parities) until the end of lactation (28 weeks), then first lactation does tended to be more persistent than multiparous does. The corresponding figures ranged from 0.71 to 0.84 percent per day during the first and fourth or greater parity, respectively. Although the term is not consistently defined in the literature, several other workers, including Sachdeva et al. (1974) and Gipson and Grossman (1990), confirm that persistency is a declining function of parity number. In their study of dairy cow lactation curves, Stanton et al. (1992) propose that the higher persistency of first lactating animals could, in part, be attributed to the maturation process that these younger animals are undergoing. The concomitant increase in milk potential over time tends to counteract the normal decline in milk yields with advancing stage of lactation. With respect to the present data, the estimated relative increase in body weight of 15.2 percent over the reproductive cycle for first lactating does, as opposed to 8.4, 1.1, and -3.4 percent in second, third, and fourth and higher parity goats, could be regarded as evidence in support of the latter interpretation.

The average yield curves estimated by Wahome et al. (1994) differed from the present results, in that their analysis revealed a highly significant difference in scale among parity-specific lactation curves, while curve shapes did not differ among parity classes. Consequently, the tendency of first parity does to exhibit a somewhat higher persistency than multiparous does as detected in the present study was not reported by Wahome et al. (1984). Also, both initial and peak daily milk yield levels were lower than that estimated in this work, with estimates of initial and peak yields ranging between approximately 230 and 395 $g \cdot day^{-1}$, and between approximately 245 and 420 $g \cdot day^{-1}$, respectively. Some of these differences may be due to the presence of multicollinearity in the ANOVA model used by Wahome et al. (1994) to derive estimates of lactation curve parameters for each level of the predictor variables considered. For instance, their model simultaneously took into account the effects of parity, litter size, and doe body weight, which tend to be correlated with each other. Model interpretation is complicated in the presence of strong linear relationships amongst the explanatory variables because the true effect may be masked by redundant predictor variables. In general, collinearity causes individual parameter estimates to be biased and less precise than would otherwise be the case if correlated predictor variables were deleted from the model (Everitt and Dunn, 1991; Jobson, 1991). Additionally, as indicated by Kowalski and Guire (1974), non-linear functions such as the one fitted to individual sequences of observations by Wahome et al (1994) do not have the convenient property shared by the class of polynomial functions employed in this study, which is that the "mean curve" fitted to the mean response values at every observational time point is equivalent to that obtained by fitting individual records to a set of such polynomials and averaging the functional coefficients. Since this is generally not true for non-linear functions, individual curves are subject to distortion through group averaging, which may oversmooth the fitted curves and mask the inherent between-subjects variability (Kowalski and Guire, 1974; Van Der Linden et al., 1970). Indeed, the present analysis revealed that inter-animal heterogeneity in milk production

potential was a major source of variation in observed milk yield profiles. Lastly, the significance levels of individual model factors reported by Wahome et al. (1984), on which they based their model selection, are likely to be invalid because the fundamental assumptions concerning the statistical independence of observations and the homogeneity of variances over time are not fulfilled. Data collected in a longitudinal study do not meet these requirements by nature (Doren et al., 1988; Cnaan et al., 1997; Kenward, 1985, 1987; Van Der Linden et al., 1970). As pointed out by Van Der Linden et al. (1970), it is precisely the dependence between adjacent observations which enables us to construct mathematical equations describing yield or growth patterns over time. The most important consequence of the lack of independence is that, due to the inflation of fixed effects test statistics, testing of the hypothesis of prime interest in a longitudinal setting, i.e., that the mean response among treatment or classification groups is the same at each measurement time is ruled out (Diggle, 1988; Doren et al., 1988; Pérochon et al., 1996).

Effect of postpartum body weight of dam

In agreement with the findings of most workers, milk yield increased considerably with postpartum body weight of dam. As already mentioned above, this is to be expected from the well documented positive correlation between milk yield and almost all body dimensions. However, the effect of body weight is likely to be confounded with other sources of variation, particularly with age and parity number. Because of the presence of multicollinearity, milk yield estimates based on models attempting to adjust for all three factors cause interpretational difficulties. On the other hand, assessing, for instance, the effect of dam postpartum body weight within parity classes may be prevented by highly unbalanced and small observation numbers. Obviously, the number of animals in the highest and lowest body weight classes will tend to be underepresented, respectively, in first lactating and multiparous dam categories. This was the case with the present data and, therefore, it was not possible to investigate whether the effect of postpartum dam body weight on milk yield was independent of that of parity. Nevertheless, the comparatively large differences in milk yield across body weight levels, in conjunction with the marginal effect of parity on milk yields could be regarded as evidence in support of this hypothesis. In their study on Red Sokoto goats, Ehoche and Buvanendran (1983) arrived at similar conclusions. These authors found that doe liveweight was the most important factor influencing milk yield, even after adjustment was made for dam age. Similarly, in his review on the effect of body conformation on production in dairy goats, Gall (1980) concludes that differences in body weight account for about 20 to 30 percent of the variation in milk yield of goats. Consistent with the present results, he also states that this relationship is most pronounced when based on weight measurements taken shortly after kidding. With respect to the inevitable correlation between dam age, dam body weight, and thus milk yield, Lampeter (1970) argues that the primary influence on milk production appears to be that of weight, and not of age acting independently of weight.

The main explanation for the increase in milk yield with postpartum body weight then rests upon the assumption that, as noted above, this trait is closely related to udder volume and mammarian tissue mass (Gall, 1980). Additionally, it may also reflect an increased capacity to buffer against the rise in metabolic requirements in relation to the lactation process. The present data revealed that when pregnancy coincided with the long dry season, the accumulation of body reserves during this reproductive stage may be insufficient to sustain the high initial milk yield levels commonly observed in goats.

Effects of mating season

The seasonal variation in forage quality and quantity was clearly reflected in the milk yield profiles according to mating season group. Similarly to McDowell et al. (in Iloeje et al. 1980), who showed that the feed component alone could account for about 30% of all variation in lactation performance, it can be assumed that with no variation in feed quality and quantity the effect of mating season would be negligible. Does kidding in the period from October to April (mating seasons 3, 4, and 5) generally had access to a higher level of nutrition and were able to sustain a higher level of milk production than does kidding in the long dry season (mating seasons 1 and 2). Does which kidded at the end of the long rains (group 6) had the advantage of a high primary productivity throughout gestation and produced the largest peak yields (580 $g \cdot day^{-1}$ attained at about 4 weeks of lactation). Scale and shape of lacation curves differed markedly between mating season groups, and the typical lactation curve shape with an initial rise to a distinct peak and a subsequent decline until the end of lactation usually observed in well nourished animals could only be seen for lactations that were initiated during or at the end of the rainy season (mating seasons 5 and 6). Similarly to the observations made by Nicholson (1984) in a pastoral herd of Boran cows in Southern Ethiopia, improvements in nutritional conditions caused a rapid rise in milk production at virtually any stage of lactation. Perhaps the most striking feature emerging from the estimated response profiles is that marked peaks in milk yield occurred as late as 22 (group 3) and 24 (group 1) weeks of lactation. In one case (group 1), maximum milk yield was reached only after 14 weeks of lactation, at which time the natural decline of

production was counterbalanced by increased forage availability at the onset of the short rains. Generally, multiple peaks in milk production are likely to be observed whenever a rainy season occurs after about the first half of the lactation period. This is in accordance with the study of Blackburn and Field (1990) noted above, who found multiple peaks in lactation curves of does which kidded during the long dry season.

Methodological issues

From the foregoing, several consequences for evaluating lactation performance in goat herds exposed to seasonally fluctuating nutrient supplies emerge. Firstly, it will generally be difficult (if not entirely impossible) to identify the principal lactation phases (ascending phase, peak, and descending phase) which commonly characterize lactation curves and on which comparative assessments of lactation performance are usually based. Moreover, when average daily milk yield curves have multiple peaks, it is not clear how such concepts as persistency or even lactation length could be meaningfully defined. Secondly, from a statistical point of view, the conclusion cannot be avoided that when the major influence on milk production is the season in which lactation is initiated, there will be little point in trying to fit smooth and well-behaved non-linear algebraic curves such as the incomplete gamma, inverse polynomial, or general exponential to lactation data. This tends to be further exacerbated by the fact that, in semi-arid regions, environmental conditions may exhibit considerable inter-year variability, so that seasonal patterns of nutrient availability cannot be expected to be fully reproducible. While under controlled environmental conditions, the form of the response-over-time curve may be suggested by theoretical considerations, this is clearly not the case in such a setting. In the absence of a mathematical form for yield curves over time that is prescribed by some theory, it appears justifiable to concentrate efforts on finding an empirical function that provides an adequate summary of the available data (Kenward, 1985; Lindsey, 1993). For several reasons, the polynomial functions used in this study are particularly useful in this respect. Firstly, they can approximate any yield pattern if a sufficiently complex model (in terms of degree of polynomial in time) is selected and enough observations over time are available to fit the specified function (Burchinal et al., 1994). Secondly, as demonstrated in this study, fitting polynomial functions in time to longitudinal data using the general linear mixed model (GLMM) approach has the advantage of yielding both individual-specific and population average trajectories, and that hypotheses regarding the relationship between response patterns and predictors of interest can be tested (Cnaan et al., 1997; Verbeke, 1997). GLMM‘s make full use of the information on the variability of the experimental unit that is contained in the data, and accommodate the correlatedness of repeated measurements in computing test statistics for the comparison of profiles (Kenward, 1987; Ware, 1985; Zeger and Liang, 1992). If the variance-covariance structure is defined correctly and the variance components estimated with sufficient precision, an immediate result of the linear mixed model approach is that the fixed-effects parameters are estimated with greater precision than if the covariance structure had been ignored (Littell et al., 1996; Rawlings and Spruill, 1994).

It should be emphasized that taking into account major environmental influences (such as the effects of mating season and range condition considered in this study) in the fitted model is not only of interest in its own right, but essentially constitutes a prerequisite for making valid inferences with regard to the impact of other predictor variables on response trajectories. In contrast to polynomial functions, non-linear functions are not well suited for modelling the mean structure, since they are less flexible and will tend to smooth-out environmental perturbations. In the context of fitting nonlinear models to growth data, in which similar problems with respect to estimation and interpretation arise, Fitzhugh (1976) states that any equation-bound method already imposes artificial mathematical constraints on the biological variation inherent in response curves. And they are certainly even less capable of capturing variations in response caused by erratic fluctuations in environmental conditions. This becomes evident when one compares the response profiles by mating season group obtained in this study with the vegetation score specific lactation curves reported by Wahome et al. (1994). The authors classified individual milk yield sequences according to *average* vegetation condition over the first 6 weeks of lactation and estimated lactation curves for each of five average vegetation condition score levels. In spite of the fallacy associated with using the arithmetic mean as a measure of central tendency for ordinal data, this approach to classifying individual lactation sequences according to environmental condition can be assumed to capture similar effects on lactation performance as the mating season treatment effect considered in the present work. The principal difference between both predictors is that the levels of the mating season variable refer to fixed points in time and as such tend to represent a smaller range of environmental states. Note, however, that the response profiles for the browse-adjusted lagged, range condition scores (RC II) estimated in this study cannot be compared to those of Wahome et al. (1994): RC (II) was entered as a sequence or time-changing effect (Lindsey, 1993) into the fitted model, and thus the response profiles for the five condition score levels give an impression of the relative effect of the vegetation state on milk production at each time point during lactation. Nevertheless, changes in the production environment throughout lactation should affect the shape of lactation curves in a similar way in both cases, with improvements in nutrient availability causing a rise in milk production and

nutritional stress during the dry season leading to a rapid decline in average daily yields. None of such patterns, including multiple peaks, were apparent in the lactation curves presented by Wahome et al. (1994). Obviously, these features were averaged out in the process of fitting the incomplete gamma function to individual lactation sequences.

5.5 Conclusions

Evaluating milk production in pastoral goat herds exposed to strong seasonal changes in forage supply is perhaps best carried out in terms of cumulative milk yields, instead of average daily yields. The present analysis has shown that cumulative production until a specified time-point can be used as a criterion for assessing the relative performance of treatment or classification groups. Turning to the question of evolution of cumulative milk production over time, this analysis has shown that, with respect to the effect of mating season, the level of peak daily yields attained during lactation are not decisive in determining overall lactational performance. For instance, while the largest peak yields were achieved by goats which kidded toward the end of the long rainy season (mating season 6), total milk production in this group surpassed that achieved in all others only until about 12 weeks of lactation. Thereafter, cumulative milk yields in group 6 levelled off rapidly due to nutritional constraints experienced during the long dry season.

With regard to the total amount of milk produced until 28 weeks of lactation, the current production system could benefit from the introduction of a restricted breeding management allowing does to be bred in the period from June to November (mating seasons 3, 4, and 5). A slightly different recommendation emerges with respect to total milk production until weaning. In this case, maximum milk production can be expected to be achieved by does mated between October and January (mating seasons 5 and 6). In contrast, joining does just prior to or during the long rainy season (mating seasons 1 and 2) is likely to lead to very poor milk production (less than 34 kg per doe until weaning). The present experiment has revealed that such low levels of milk output are insufficient to promote adequate liveweight development of kids until weaning (Chapter 4). Similarly, the failure to provide sufficient milk to the kids during this stage has also been found to significantly increase the incidence of early kid deaths (Chapter 3).

Chapter 6

An approach to steady state productivity assessment in livestock herds based on stage-structured matrix population models and mathematical programming

6.1 Introduction

In agricultural production planning, the concepts of technical and allocative efficiency play a key role in guiding decisions relating to resource allocation (Rehman, 1982). Efficient allocation of resources in production requires the definition of an objective, in relation to which different decision alternatives can be evaluated. Technical efficiency relates to the maximum physical output attainable for a given level of production inputs, given the range of alternative technologies available to the producer. Assessing technical efficiency thus can help in choosing the most appropriate technology for production. It should, however, be kept in mind that within the framework of the neo-classical theory of the firm, the achievement of technical efficiency is a necessary, but not sufficient condition to ensure economic efficiency (Ellis, 1993). In livestock-related research, a confusing multitude of different measures of technical efficiency have been used in the past, some of which have been reviewed by Baptist (1992b) and more recently by Bosman et al. (1997*a*). The former author identified the failure to distinguish between production level and productivity as defined above as a major deficiency shared by many of the productivity measures commonly applied in animal production science. Typically, to evaluate efficiency at the herd level such indices relate gross output per time unit in terms of monetary value, mass or energy to the number of animals (or their total liveweight, or metabolic liveweight) required to produce it. Examples encompass the so-called ILCA livestock productivity indices (Wilson et al., 1985), which have been widely used for productivity assessments in African livestock production systems. The implicit assumption that is made when using this type of biological efficiency measure is that there exists a constant relationship between the denominator of the index (e.g., the total number or total liveweight of dams that produced the output) and input costs, among which the most important are commonly feed costs (Upton, 1993; Morris et al., 1994; James & Carles, 1996). However, such an assumption is questionable when making comparisons among different species, breeds within species, or between herds of the same breed maintained under different environmental or management conditions. Furthermore, even within a given livestock herd, feed requirements are not constant but vary with age, reproductive status, or life cycle stage. In order to circumvent these problems, Baptist (1992*a*), Upton (1993), Morris et al. (1994), as well as James and Carles (1996) have proposed the use of feed or feed energy inputs as a scaling factor in calculating livestock productivity measures. When valuing feed inputs in terms of their energy content, the underlying assumption is that, *ceteris paribus*, once the energy requirements for all physiological functions are met, so are all non-energy requirements (Konandreas and Anderson, 1982).

However, relating outputs produced to the level of input use is not the only requirement that must be met to obtain reliable estimates of biological efficiency. Two more fundamental aspects which, when ignored in computing efficiency measures, can lead to questionable results in livestock herd productivity assessments, need to be taken into account. These relate to the effects of herd structure and dynamics on the calculation of efficiency measures. Firstly, changes in performance (i.e., survival, reproduction, and yield levels) over successive life cycle stages cause the computation of biological herd productivity measures to depend on herd structure at the time of assessment. Hence, unequal stage abundances among the herds or alternatives which are to be compared will tend to lead to biased assessments. Secondly, allowance has to be made for breeding stock replacements if the herd is to be maintained at its current level of productivity (Upton, 1993). Herd dynamics and structure is determined not only by inherent age- or stage-specific fitness traits, but also by the offtake policy, i.e., by the choice that is made between immediate consumption and investment in future herd growth.

Steady state herd growth models can accomodate for the above effects on calculated efficiency measures by considering sustained self-recruiting herds, in which herd size and structure are maintained in an equilibrium state over time. Previously published approaches to steady state herd productivity assessment are based on an age-structured description of herd dynamics (Put et al., 1987; Baptist, 1992; James & Carles (1996); Upton, 1989, 1993). However, the demography of domestic livestock species may depend on size or developmental stage much more than on age (e.g., parity or size), and often these variables are only weakly correlated with

age. A further limitation of available computer implementations of the concept of steady state productivity assesment in livestock herds (Baptist, 1992*a*; James & Carles, 1996) is that performance traits cannot be made dependent on the age an animal has reached in its species-specific life-cycle. Vital parameters and performance traits of breeding females such as fecundity, litter size, milk yield, liveweight and liveweight gain are assumed to remain constant throughout the productive lifespan. Additionally, these computer programs often totally lack the capability of optimizing the culling policy that leads to a steady state in herd size and structure, e.g. for LPEC (James & Carles, 1996). The program PRY developed by Bapitst (1992*a*) allows only the optimization of parts of the culling regime (optimal culling age for surplus animals; cull-for-age threshold for breeding females), so that one has to rely on heuristic rules to optimise other parts (selective culling of breeding females).

In order to refine the concept of steady state herd productivity assessment and improve its flexibility and applicability, the present chapter explores an alternative method of modelling herd dynamics over time and of deriving optimal steady state herd structure and culling policies. The proposed procedure combines results from population dynamics theory (Caswell, 1989), with methods for the factorial assessment of feed energy requirements of livestock, and basic results from optimal harvesting theory of multicohort populations (Williams, 1989). Herd dynamics are described through a deterministic, density-independent, discrete time model which predicts subsequent stage distributions of a population of breeding females and their male and female offspring for an initial stage/sex distribution and corresponding sets of stage specific survival and fecundity rates. The optimum sex and stage-specific culling policy is derived by translating the population dynamics model into a non-linear programming problem. The (non-linear) function to be maximized is the energetic or ecological efficiency (total gross energy produced per unit of metabolizable feed energy input per time unit) of the herding enterprise. Maximization is performed subject to the constraint that total herd size and structure remain constant over time. Although attention is focussed on grazing ruminant livestock, the method can readily be extended to non-ruminant livestock species or intensive husbandry systems.

In the following sections, the theoretical background and the procedure used to assess herd productivity is developed. To make the approach transparent, some basic results from population dynamics theory are presented first, beginning with the formulation and parametrisation of an age-structured matrix population model. Stage-structured matrix population models, which form the basis of the present herd growth model, are introduced thereafter, followed by a description of the procedures applied in calculating herd feed energy requirements and energy outputs. Finally, the optimization procedure used to derive optimal culling policies and stage abundances at the steady state of population dynamics are presented, followed by a discussion of the modelling approach. For a detailed description of a practical application of the proposed methodology, reference is made to Chapter 7.

6.2 Stage-structured matrix population models and their parameterisation

A population can be defined in general terms as a group of individuals coexisting at a given moment. Demographic analysis proceeds by first focusing on the individual (and its demographic attributes) as a natural unit. The fundamental traits considered at the level of the individual are birth, development, maturation, reproduction and death. Developmental processes cause individuals to differ in these traits depending on their age, size or developmental stage. The latter mechanisms can be used to group individuals in a population into several cohorts, which are formally defined as groups experiencing the same event in a particular time period (Pressat (1985), cited in Carey (1992)). The explicit consideration of individual differences by categorizing organisms according to some characteristic leads to the definition and identification of population structure (Caswell, 1996a). The sequence of transitions from one cohort to another and the duration of residence in each cohort define the life cycle of the organism.

The most obvious and widely used classification of individuals in a population is by age cohorts, where exact or chronological ages are grouped into periods or "classes". Classical demographic analysis is based on an age structured approach to population dynamics and uses a system of tabulating age-specific survival and reproduction known as life and fecundity tables (hereafter referred to generically as the life table). In what follows, density dependent effects on vital rates as well as demographic stochasticity, i.e. deviations from model projections due to finite population size will be ignored. The basic entry in the life table is the survivorship function:

$$l(x) = P[\text{survival from birth to age } x] \tag{1}$$

A number of other life table statistics, such as survival and mortality rates, the distribution of age at death, life expectancies etc., can be calculated from the survivorship function $l(x)$ (see Caughley (1977) and Carey (1992) for further details). Reproduction is described by the maternity function:

$$m(x) = \text{E[offspring per individual aged } x \text{ per time unit]} \quad (2)$$

$m(x)$ is usually expressed in terms of female offspring produced per female aged x time units, but can be expanded to include male offspring in two-sex models. For the sake of simplicity, only the female part of the population is considered here. In order to translate the life-table results into a discrete time matrix population model, the continuous age variable x must be divided into discrete age classes, i=1, 2,..., k of equal duration. By convention, age class i corresponds to ages $i-1 \leq x < i$. For a chosen time step, t, the number of individuals in, or abundance of, each age class can then be projected from one time to the next using a set of first-order difference equations. Let $n(t)$ represent a column vector of the abundances of the k age classes at time t, and denote by f_i, i=1, 2,..., k, the number of newborns (or age class 1 individuals) produced at time t+1 per individual present in age class i at time t. The number of individuals in each of the k age classes at time t+1 are

$$n_i\ (t+1) = p_{i-1}\, n_{i-1}\ (t) \quad for \quad i = 2, 3, ..., k \quad (3)$$

$$n_1\ (t+1) = \sum_{i=0}^{k} f_{i-1}\, n_i\ (t) \quad (4)$$

where p_{i-1} is the survival probability of members of age class $i-1$ over the time interval [t, t+1]. The system of first-order difference equations specified by equations (3) and (4) can be written in matrix form

$$\begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ \vdots \\ n_k \end{pmatrix}(t+1) = \begin{bmatrix} f_1 & f_2 & f_3 & \cdots & f_k \\ p_1 & 0 & 0 & \cdots & 0 \\ 0 & p_2 & 0 & \cdots & 0 \\ \vdots & \ddots & \ddots & \cdots & \vdots \\ 0 & 0 & \cdots & p_{k-1} & 0 \end{bmatrix} \cdot \begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ \vdots \\ n_k \end{pmatrix}(t)$$

or, more compactly

$$n(t+1) = \mathbf{A}\, n(t) \quad (5)$$

In the context of age-classified population analysis, the population projection matrix **A** is often referred to as a Leslie matrix (Leslie, 1945). Iterative postmultiplication of **A** by the age abundance or population structure vector $n(t)$ projects the future state of the population.

The parameters in the population projection matrix can be derived from life table data. Before proceeding, we make a distinction between birth flow populations, in which births occur continuously over time and birth pulse populations, in which reproduction is concentrated in a short breeding season. These two patterns of reproduction produce very different distributions of individuals within age classes, and lead to different approximations for the survival probabilities (Caswell, 1989). In what follows, births are assumed to occur at one point during the projection time interval so that the population is of the birth pulse type. Note that this assumption does not preclude overlapping of generations, a typical feature of many long-lived organisms. Also, it is supposed that within each time interval the population is censused immediately after reproduction. Such a "postbreeding census" implies that all birth events within the interval [t, t+1] occur at t+1, i.e. at the beginning of the next time period. All newborns (age class i=1) are therefore of age $x=i-1=0$ at census time.

Since the life-table functions $l(x)$ and $m(x)$ are continuous, the discrete time coefficients in the projection matrix have to be approximated. The derivation of the formulas presented below for estimating survival probability and fertility entries are given in Caswell (1989). When population census is carried out just after reproduction, the survival probabilities p_i in matrix **A** can be estimated by

$$p_i = l(i+1)/l(i) \quad (6)$$

Note that every individual in age class i is of the same age $x=i-1$, so that p_i represents the probability of survival from age $x=i-1$ to age $x=i$. The birth pulse fertilities f_i are estimated using the reproductive output produced by an individual of age i upon reaching its ith birthday, and the probability of surviving until reproduction, p_i:

$$f_i = p_i m_i \quad (7)$$

Thus, the fertility coefficients f_i are the *expected* reproductive outputs per individual of age i in the population during each time interval. In livestock herds, fecundity in fertile females can be assumed to be a function of prolificacy, breeding female survival until parturition, and survival of the fetus until birth.

The age-structured population model considered so far implicitly assumes that properties other than age are irrelevant to an individual's demographic fate. If vital rates (i.e. rates of survival, growth, and reproduction) also depend on factors other than chronological age, these must either be highly correlated with age or the distribution of age cohorts among the relevant categories must be stable. However, the demography of livestock herds, like that of many other organisms, can depend on size or developmental stage much more than on age, and these variables are often only poorly correlated with age (Caswell, 1989; Getz and Haight, 1989). Situations may also occur in which the age of individual animals is difficult to determine accurately, but other characteristics such as body size, reproductive status, or parity number may be more convenient to measure and more pertinent to questions relating to population dynamics (e.g., Wu and Botkin, 1980; Crouse et al., 1987; Escos and Alados, 1994).

A generalisation of the Leslie matrix model, known as the Lefkovitch population projection matrix (Lefkovitch, 1965), allows the categorization of the life cycle of organisms into life stages other than age classes and the projection of future population states. In the Lefkovitch matrix, stage definitions are not required to be related to chronological age of individuals. The method, however, is very flexible since it allows the consideration of individuals classified both by stage and age. This is important in situations where the vital rates change as a function of life cycle stages and of age within stage categories (e.g., Goodman, 1969; Law, 1983). The fundamental assumption of Lefkovitch-type models is that all individuals in a given category are subject to identical mortality, growth, and fecundity schedules (Crouse et al., 1987).

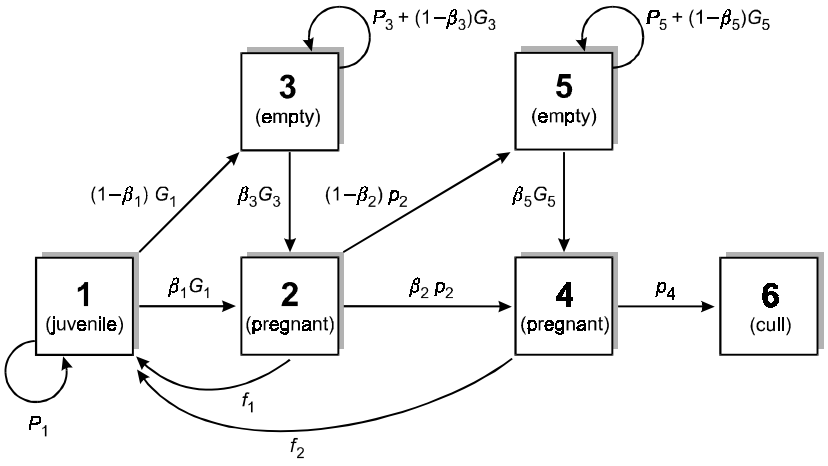

Figure 6.1. Life cycle graph of breeding females of a hypothetical livestock species.

A graphical description of a hypothetical stage-structured livestock population is given in Figure 6.1. The structure of the so-called life cycle graph (Caswell, 1989) and the resulting transition matrix depend on the projection time interval chosen. Each node n_i (i=1, 2, 3, 4, 5, 6) in the graph defines a stage in the life cycle of the population. Let us assume that the life cycle graph describes the dynamics of the female portion of a livestock herd and that breeding females are mated once a year, starting at the end of the juvenile stage numbered 1, and that all individuals are culled (or die) after giving birth a second time upon reaching stage 6 (recall that in a birth pulse population all breeding and birth events within an interval $[t, t+1]$ occur at $t+1$). Also, the projection time step is assumed to be equal to the one year duration of pregnancy. Then, an arc connecting two nodes n_i and n_j indicates that an individual in stage i at time t can contribute (by development or reproduction) individuals to stage j at time $t+1$. Self-loops are of unit time length and indicate that individuals in that stage at time t can contribute individuals to the same stage at time $t+1$. The coefficients labelling the arcs define the number of individuals to be observed in stage j at time $t+1$ per individual present in stage i at time t.

Upon reaching reproductive maturity at, for example, 3 years of age, stage 1 individuals may, conditional upon survival, either conceive and grow into pregnancy stage 2, or remain empty and move into stage 3. (Note that all juvenile females are assumed to be used as replacements. How to take into account the decision to rear part of this cohort as surplus animals will be discussed further below). For each stage 2 and 4 individual a number f_1 and f_2 of young is expected to be born at the end of the year (note that the survival of

dams enters into the calculation of the f_i's). At the beginning of the following year, immediately before census time, the surviving stage 2 and 3 individuals breed again and, if they conceive, make the transition into stages 4 (for stage 2 individuals) or 2 (for stage 3 individuals). Alternatively, stage 2 and 3 individuals may survive without becoming pregnant and therefore grow into stage 5 or remain in stage 3, respectively. It is assumed here that animals which are susceptible to pregnancy (stages 3 and 5) have to remain at least until the next breeding season in the same stage before they can conceive and move into one of the two pregnancy stages. The average residence in stages 3 and 5 is thus determined by the probability of conception. Individuals in stage 4 survive until the next year with a probability p_4, become stage 6 individuals upon giving birth, and are culled (or die) thereafter.

The G_i and P_i coefficients in Figure 6.1 are transition probabilities defining the probability of surviving and growing into the next stage class, and of surviving and remaining in the same stage, respectively. These depend upon the stage durations, d_i, and the stage-specific probabilities p_i of surviving from time t to t+1. Except for the probabilities of surviving and remaining in the same stage (P_i) and the probability of surviving into stage 6 (p_4), all transitions in the graph are conditioned upon conception (β_i), so that the final *joint* transition probabilities are obtained as the product of the marginals, i.e. $\beta_2 p_2$; $(1-\beta_2)p_2$; $\beta_i G_i$; and $(1-\beta_i)G_i$ (it is assumed here that the marginal probabilites are independent of each other). Since no self-loop is present at stage 2, in this case transitions are only a function of survival and conception (β_2 and p_2). As before, the f_i's represent reproductive outputs, i.e. the expected number of offspring produced per individual in stage i at time t and observed at census in stage j at time t+1. The stage-structured transition model depicted in the life cycle graph can be translated directly into the population projection matrix **A** in equation (5). The projection matrix corresponding to Figure 6.1 is

$$\mathbf{A} = \begin{bmatrix} P_1 & f_1 & 0 & f_2 & 0 & 0 \\ \beta_1 G_1 & 0 & \beta_3 G_3 & 0 & 0 & 0 \\ (1-\beta_1) G_1 & 0 & P_3 + (1-\beta_3) G_3 & 0 & 0 & 0 \\ 0 & \beta_2 p_2 & 0 & 0 & \beta_5 G_5 & 0 \\ 0 & (1-\beta_2) p_2 & 0 & 0 & P_5 + (1-\beta_5) G_5 & 0 \\ 0 & 0 & 0 & p_4 & 0 & 0 \end{bmatrix} \quad (8)$$

To summarise, the main differences between age- and stage-structured matrix population models are that the stage classes may differ in their duration and that individuals may also remain in the same stage from one time to the next. In order to parameterise the stage-based matrix model, the single time step survival probabilities p_i and the fertility coefficients f_i can be estimated from longitudinal stage-specific survival and fecundity data. A different approach has to be adopted for estimating the marginal stage probabilities of surviving and growing into the next stage (G_i), and of surviving and remaining in the same stage (P_i), since they depend on stage-specific survival rates and on the duration of each stage, d_i. The stage duration itself can be influenced by physiological or sexual maturation processes. For instance, sexual maturation determines the duration of the juvenile stage (assumed to last 3 years), d_1 , in Figure 6.1. For the hypothetical population dealt with here the stage duration is fixed and corresponds to the length of three time steps (3 years) for juveniles, and one time step for all other stages having self-loops. The latter is true because one time step was assumed to be equal to both the duration of pregnancy and the time period between successive breeding seasons. In general, when the stage duration can be assumed to be fixed the transition probabilities P_i and G_i can be approximated as (Crouse et al., 1987; Caswell, 1989):

$$P_i = \left(\frac{1-{p_i}^{d_i-1}}{1-{p_i}^{d_i}} \right) p_i \quad (9)$$

$$G_i = \frac{{p_i}^{d_i} (1-p_i)}{1-{p_i}^{d_i}} \quad (10)$$

Since d_i=1 for i=3, 5 in Figure 6.1, the transition probabilities for these stages reduce to

$$\left. \begin{aligned} P_i &= p_i \\ G_i &= p_i \end{aligned} \right\} \text{for } i = 3, 5$$

As with the age-structured population model presented above, numerical projection by repeated matrix multiplication is the simplest form of analysis that can be performed with this type of demographic model. However, projecting a population into the future is of limited value, since the stage abundances at any time will dependent on the initial conditions specified by the stage abundance vector $n(t_0)$. More general and widely applicable conclusions can be drawn by applying analytical approaches based on matrix algebra. Eigenanalysis provides expressions for calculating the stable stage distribution, the finite rate of increase of the population, and the reproductive value of an individual in a given stage (see Caswell (1989) and Cochran & Ellner (1992) for further details).

When the projection matrix **A** is non-negative, primitive, and irreducible, then it satisfies the necessary conditions for the Perron-Frobenius theorem (see Caswell (1989), Chapter 4). According to this theorem, a matrix having these properties has at least one positive latent root. The largest such root, usually denoted by λ, is known as the maximal root or dominant eigenvalue of the projection matrix **A**. The dominant eigenvalue is a scalar value which expresses the multiplicative effect of the projection matrix **A** on the stage abundance vector $n(t)$, and thus gives the asymptotic rate of population growth. The right eigenvector **w** corresponding to λ is defined by

$$\mathbf{Aw}=\lambda\mathbf{w} \tag{11}$$

and represents the stable stage distribution to which the population will ultimately converge. Independently of the initial stage structure the population abundance vector $n(t)$ will, after a sufficient number of projection time steps, approach the stable stage distribution **w**, where each stage class increases in size by a factor equal to λ each time period. The reproductive values of the stage classes are given by the left eigenvector **v** corresponding to λ. The left eigenvector satisfies the equation

$$\mathbf{vA}=\mathbf{v}\lambda \tag{12}$$

The reproductive value of a stage class is a measure of the potential contribution of an individual in that stage to future population growth, and is a function of the amount of future reproduction, the probability of surviving to realize it, and the time required for the offspring to be produced (Caswell, 1989). For comparative purposes the elements of the right eigenvector **w** are rescaled so that they sum to 1 and express the proportional abundance of individuals in each stage class at equilibrium. Likewise, the reproductive values in **v** are usually expressed in relation to the newborn stage whose reproductive value is set to 1.

An important part of the analysis of the projection matrix is to investigate how the finite rate of increase λ would be affected by changes in the vital rates or, alternatively, how important each stage class is in determining population growth rate. These information are valuable for assessing the impacts upon λ of errors in estimation, alternative management strategies, and environmental perturbations (Crouse et al., 1987; Caswell, 1989, 1996*b*). The sensitivity of λ to a change in the a_{ij}th element of **A** when all other elements are held constant is

$$\partial\lambda/\partial a_{ij}=v_i w_i/\langle\mathbf{w},\mathbf{v}\rangle \tag{13}$$

where v_i and w_i are the *i*th element of the reproductive value vector and *j*th element of the stable stage distribution vector, respectively, and $\langle\mathbf{w},\mathbf{v}\rangle$ is the scalar product of the two vectors. The sensitivity of λ gives the effect of a small additive change in one of the vital rates. The effect of a small *proportional* change in a vital rate can be assessed through the elasticity of λ:

$$e_{ij}=\frac{a_{ij}}{\lambda}\frac{\partial\lambda}{\partial a_{ij}} \tag{14}$$

The e_{ij} sum to 1 and also measure the proportional contribution of each of the matrix coefficients to overall population growth rate (Caswell, 1996*b*).

For analytical purposes, a number of useful *age*-classified statistics can also be derived for stage-structured matrix population models (see Cochran and Ellner, 1992). These comprise age-based life history traits such as the mean age at first reproduction, the probability of surviving until time at first reproduction, and the net reproductive rate, as well as age-based measures of population dynamics such as the generation time. The computational formulas for these parameters are given by Cochran and Ellner (1992). The mean age at first reproduction is the average age at which a newborn individual enters a stage with positive fecundity. It can be conceived as an average over a cohort of newborns which do not all necessarily follow the shortest possible path to a stage with positive fecundity (e.g., individuals may stay for several time steps in stage 3 in

Figure 6.1). The net reproductive rate, usually denoted by R_0, is the expected number of offspring produced by an (female) individual over its lifespan. And the generation time can be defined as the mean age of the parents of offspring produced in the current time period, once the population has reached stable stage distribution.

So far, the exposition has concentrated on describing the approach used to model the dynamics of the breeding female part of a livestock herd. Principally, incorporating stages for female and male surplus animals into the life-cycle graph in Figure 6.1 is straightforward. Since surplus animals have by definition zero fertility they form sequences of stages with only one-way communication, i.e. there is no pathway back to the part of the life cycle that does reproduce. Therefore, it is relatively easy to describe the dynamic behaviour of the surplus part of a herd, and both stage and/or age classified matrix methods for population analysis can be used to model the dynamics of surplus cohorts over time, as demonstrated

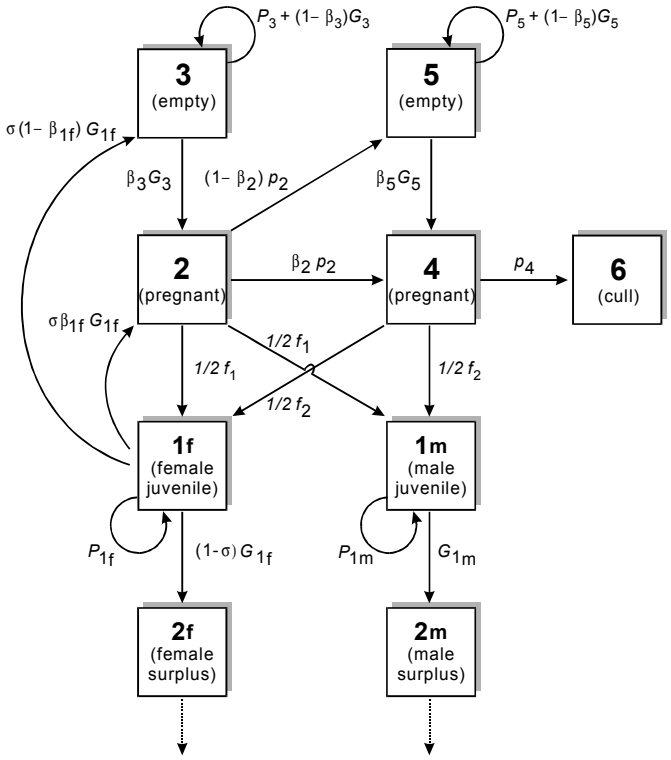

Figure 6.2. Modified life cycle graph of a hypothetical livestock species taking into account male juveniles (stage 1m) and female and male surplus stages (2f and 2m). The parameter σ denotes the fixed proportion of female immatures that are to be reared as breeding females. A sex ratio of unity was assumed at birth.

in Figure 6.2. In order to be able to incorporate a female surplus cohort into a matrix population model, one has to introduce an additional parameter, say σ, which represents the fixed proportion of females surviving the juvenile stage which are to be reared as breeding females. This introduces an element of decision-making which usually is absent in conventional applications of matrix population models. Further below, the decision to rear female youngstock as breeding females or surplus animals will explicitly be taken into account in the derivation of steady state optimal culling policy and herd structure. Note, however, that the analytical approaches based on Eigenanalysis described above cannot be applied to such a transition matrix, since it necessarily contains stages that make no contribution to some other stages, and hence is reducible.

6.3 Procedure for estimating feed energy requirements at the herd level

For the purpose of illustrating the calculation of total feed energy required at the herd level per projection time unit, only the body functions maintenance, growth, lactation, and pregnancy are considered here. However, the principles behind the formulas presented can easily be extended to other functions such as draught power or wool and hair production. Ideally, total forage consumed by the herd per time unit, as well as quality of forage on offer should be measured in the field as a basis for calculating the input in terms of

metabolizable energy (ME) utilized for achieving an observed level of performance. This, however, seems to be impracticable and thus an alternative approach has to be devised. James and Carles (1992) proposed to estimate total feed intake in terms of metabolizable energy indirectly, by using standard ration formulae to calculate the quantity of metabolizable energy animals must have obtained in order to achieve the observed level of performance. This procedure can be adopted in the present context to estimate feed energy requirements per time unit of livestock herds.

In assessing feed energy requirements, an account has to be taken of the fact that not all individuals present at the beginning of a time interval survive until its end. ME requirements per animal over a single time interval have therefore to be corrected for mortality. This requires the knowledge of survival curves for each life history stage. Then, an appropriate assessment of stage-specific ME requirements for each body function over the interval [t, t+1] consists in summing together the *daily* requirements for each body function for all days a within [t, t+1], weighted by the probability of surviving until day a, $t \le a \le t+1$. However, if necessary the projection time interval can also be devided into intervals of length l, covering several days or weeks. The expected ME requirement for maintenance, growth, lactation, and pregnancy R_{ij}, of an animal in stage i at time t over the projection time interval [t, t+1], of length L days, can be calculated as

$$R_{ij} = \sum_{a=1}^{n} r_{ij}(a) \cdot p_i(a) \tag{15}$$

where

a = is the number of the time interval of length l (in days) since the start of interval [t, t+1], with $1 \le \alpha \le L/l$.

$r_{ij}(a)$ = is the mean ME requirement of an animal in stage i over period a for the jth body function.

$p_i(a)$ = is the conditional probability that an individual in stage i alive at the start of time period a within [t, t+1] survives until the end of a.

j = maintenance, growth, lactation, or pregnancy.

The $r_{ij}(a)$'s have to be computed from stage-specific growth and lactation curves. The time axis of each curve first must be discretized into n consecutive time periods. Stage-specific *average* daily values for body weights, body weight gains, and lactation yields ($Y_{ij}(a)$) within each period a can for example, be obtained by linearly interpolating estimates at the start and end of the period:

$$Y_{ij}(a) = \frac{y_{ij}(a-1) + y_{ij}(a)}{2} \tag{16}$$

Note that interpolation becomes necessary only when l>1day. Finally, the mean ME requirement of an animal in stage i over period a for the jth body function can be calculated with the following formula:

$$r_{ij}(a) = Y_{ij}(a) \cdot ME_j \cdot l \tag{17}$$

where

ME_j = is the daily ME requirement per unit of body function j.

A slight modification of equation (15) is necessary for stages with self-loops, since here, stage durations exceed the length of one projection time step. The effect is that stage abundances at the start of each time interval consist of a mixture of individuals recruited from other stages and of individuals that survived the previous time step and remained in the present stage. However, the expected ME requirements over [t, t+1] for an individual present at time t can be approximated from total ME requirements for the entire stage duration and the probability of surviving and remaining in the same stage, P_i:

$$R'_{ij} = (1 - P_i) \sum_{a'=1}^{m} r_{ij}(a') \cdot p_i(a') \tag{18}$$

where

a' = is the number of the time interval of length l (in days) since the start of stage i, with associated stage duration d_i, and $1 \le a' \le d_i/l$.

$r_{ij}(a')$ = is the mean ME requirement of an animal in stage i over the a'th period for the jth

body function.

$p_i(a')$ = is the conditional probability that an individual in stage i alive at the start of time period a' within d_i survives until the end of a'.

j = maintenance, growth, lactation, or pregnancy.

As before, equations (16) and (17) can be used to compute the $r_{ij}(a)$'s. Thus, on average, a fraction of $(1-P_i)$ of the expected ME requirements per stage must be available, over a single projection time interval, to animals in stages with positive probability of remaining in the same stage in subsequent time periods.

Energy released from mobilization of body reserves can be taken into account when calculating total ME requirements for each life history stage per time unit. In grazing livestock, substantial weight losses usually occur soon after parturition, but are also common in situations of low or declining quantity and quality of forage on offer. Similarly, the expected amount of energy available to youngstock from milk consumed until weaning could also be accounted for in calculating total metabolizable feed energy requirements per progeny present at the beginning of the juvenile stage. Both of these quantities would effectively reduce the calculated total amount of ME from feed resources that must have been available to cover observed maintenance, pregnancy, and/or lactation requirements.

6.4 Procedure for estimating herd outputs

To simplify the presentation, herd output is solely defined in terms of total meat and milk offtakes for human consumption per projection time interval, valued at their gross energy contents. Details of the method for deriving optimal culling policies are given in the next section below. For the purpose of describing the method of estimating energy contents in outputs, suffice it to say here that live animal offtakes by stage class, $u_i(t)$, are assumed to take place at the beginning of each time interval. For each life cycle stage, body weight estimates for animals present at the beginning of each time step are needed.

Using gross energetic values for protein (GE_P) and fat (GE_F), the following formula is a simple method for estimating gross energy yield per live animal offtake in life cycle stage i

$$GE_{EBWT,i} = PPFAT_i \cdot EBWT_i \cdot GE_F + PPROTEIN_i \cdot EBWT_i \cdot GE_P \quad (19)$$

where

$EBWT_i$ = is the empty body weight (kg) of an animal at the beginning of stage i.

$GE_{EBWT,i}$ = is the gross energy yield in empty body per live animal offtake in stage i.

$PPFAT_i$ = is the proportional fat content per kg $EBWT_i$.

$PPROTEIN_i$ = is the proportional protein content per kg $EBWT_i$.

Similarly to the assessment of energy requirements, milk yield and milk offtake per animal present at the start of a time interval [t, t+1] in lactation stage i has to be adjusted for mortality. Upon making appropriate assumptions with respect to the dry matter content and energetic value per unit weight of fresh milk, energy yield from milk offtake per animal present at the start of the time interval [t, t+1], in lactation stage i, can be assessed as

$$GE_{milk,i} = O_m \cdot GE_m \cdot (1-P_i) \sum_{a'=1}^{m} y_i(a') \cdot p_i(a') \quad (20)$$

where

a' = is the number of the time interval of length l (in days) since the start of lactation stage i, with associated stage duration d_i, and $1 \le a' \le d_i/l$.

$y_i(a')$ = is the total milk yield per animal in stage i in period a'.

$p_i(a')$ = is the conditional probability that an individual in stage i alive at the start of time period a' within d_i survives until the end of a'.

O_m = is the milk offtake rate per projection time period.

P_i = is the probability of surviving and remaining in the same stage i at the beginning of the next projection time period.

6.5 Derivation of steady state optimal culling policy and herd structure

The mathematical programming model for evaluating steady state culling and replacement policies, as well as overall productivity in livestock herds, is based on the matrix population model described above. The problem of finding the best combination of offtake decisions for each of the stages in the life cycle that maximizes a given index of performance, and satisfies a specific set of constraints, falls into the realm of population harvesting theory (see Getz and Haight, 1989, for a comprehensive exposition of this subject). Both age- and stage-structured matrix population models have been widely used to address questions relating to optimal harvesting of populations (e.g., Usher, 1966; Beddington and Taylor, 1973; Doubleday, 1975; Rorres, 1976, 1978; Magshoodi and Grist, 1995; Forsberg, 1996; Jensen, 1996). Doubleday (1975) was the first to show that, under certain conditions, harvesting problems in matrix population models are essentially linear, and can therefore be formulated as standard linear programming problems.

Within the framework of steady state herd growth modelling dealt with here, the management control (i.e., removing or culling individuals from the herd) imposed on herd dynamics must be such that herd size and structure remain unchanged, or in a steady state, over time. Subject to this constraint, a stage-structure and culling policy may be chosen to maximize a specific index of performance. Since the matrix population model describing herd dynamics is discrete in time, it is necessary first to specify exactly when the removal of individuals occurs with respect to the process of reproduction and stage transition. Two culling schedules are available; the first is to remove animals before reproduction, and the second to cull animals immediately after they have reproduced. With respect to the discrete time scale, pre-reproductive culling occurs immediately after the start of a new time interval at time t, whereas post-reproductive culling occurs at the end of a time interval, just prior to time t+1.

As has been shown by Doubleday (1975), post-reproductive culling is generally more efficient than pre-reproductive culling, since in the former case individuals are allowed to reproduce just before they are removed from the herd. However, for the specific life cycle of grazing animals considered here, a post-reproductive schedule would lead to unreasonable management policies. For instance, it would be possible to remove breeding females at the end of a pregnancy stage, just after parturition. Therefore, in what follows a post-reproductive culling regime is assumed to be imposed.

Let us first suppose that we are concerned with the question of choosing a set of offtake strategies to maximize a given objective functional over some time period [0, T]. Then, a culling policy consists of a sequence of offtake decisions $u(t)$ made in each time period [t, t+1], so that the dynamics of the herd can be described by

$$n(t+1) = \mathbf{A}[n(t) - u(t)] \tag{21}$$

Where $n(t)$ and $u(t)$ are respectively, a k-dimensional column vector of stage abundances, and a k-dimensional column vector specifying the number of individuals removed from each life cycle stage i (i=1, 2, ...k) at time t. **A** denotes the stage transition matrix as defined, for example, by (8). For consistency, it is required that the number of animals removed from each stage be less than or equal to the stage abundance:

$$0 \le u(t) \le n(t) \tag{22}$$

In (22), offtakes are constrained to be non-negative, thus implying that we are considering a closed herd without, for instance, the possibility of introducing animals from external sources into the herd. Further below, this condition will be relaxed. The next step is to formulate an appropriate objective function relating to the management of a herd modelled by equation (21). Generally, the performance index, I, in each time period will be a function of both stage abundance and offtake at time t:

$$\boldsymbol{I} = \boldsymbol{I}[n(t), u(t), t] \tag{23}$$

Since the problem is a dynamic one, the objective functional will then consist of maximizing the sum of individual rewards $I(n(t), u(t), t)$ obtained in each time period over the planning horizon T:

$$\boldsymbol{J}(u) = \sum_{t=0}^{T} \boldsymbol{I}[n(t), u(t)] \tag{24}$$

In summary, the optimization problem may then be written as

$$\max_{u} \boldsymbol{J}\,(u) = \sum_{t=0}^{T} \boldsymbol{I}\,[n(t), u(t)]$$

subject to

$$n(t+1) = \mathbf{A}[n(t) - u(t)]$$
$$0 \le u(t) \le n(t)$$
$$n(0) = n_0 \tag{25}$$

The value of J in this problem depends on the length of the planning horizon T, and on the initial stage distribution vector of the herd, n_0 (Mendelssohn, 1976; Getz and Haight, 1989). The dependencies on T and n_0 may be removed upon imposing further constraints on the stage abundance vector $n(t)$. For example, an additional management objective might be to keep total herd size and structure at the same level for all $t \in [0, T]$, which is also the condition required to model steady state herd productivity as defined previously, so that

$$n(t+1) = n(t) \tag{26}$$

In fact, upon introducing this steady state condition, the dynamic optimization problem (25) reduces to a static one, in which the single period optimality index $I(n(t), u(t), t)$ is to be maximized (Williams, 1989). Furthermore, the dependence upon the initial stage distribution can be eliminated by requiring that the herd be kept at a stationary population level c:

$$\sum_{i=1}^{k} n_i\,(t) = \boldsymbol{c} \tag{27}$$

The optimization problem becomes

$$\max_{u} \boldsymbol{I}\,[n(t), u(t)]$$

subject to

$$n(t+1) = \mathbf{A}\,[n(t) - u(t)]$$
$$n(t+1) = n(t)$$
$$\sum_{i}^{k} n_i\,(t) = \boldsymbol{c}$$
$$0 \le u(t) \le n(t) \tag{28}$$

Note that this problem can only be solved for $u(t)$ if $\mathbf{A}$ has a dominant eigenvalue that satisfies $\lambda \ge 1$. The solution, or optimal stationary culling policy, u^* to the optimization problem is such that the herd is kept in stationary state with respect to herd structure and size (Doubleday, 1975; Williams, 1989). In addition, the problem can be solved by standard linear programming methods, as long as the objective functional $I[n(t), u(t), t]$ is linear. The formulation in (28) is thus a straightforward way of determining simultaneously the optimal culling policy that maximizes a given performance index and the associated stable stage distribution of the herd that will be achieved at a specific level of total herd size.

The more general type of constraints as in (27) allows the taking into consideration of such things as input resource constraints, production costs, stages from which no animals are to be removed, minimum offtake levels from specific stages, and so forth. Rorres (1976) has shown that these constraints are crucial in determining the structure of the optimal offtake vector u^*. Particularly, if a number q, q=1, 2,...., m, $0 \le m \le k$, of constraints of the type

$$\sum_{i=1}^{k} d_i \cdot n_i\,(t) \left.\begin{matrix} \le \\ = \\ \ge \end{matrix}\right\} \boldsymbol{e} \tag{29}$$

(where the d_i and e are a given set of k coefficients and a given scalar value, respectively) are imposed, at most q of the k stages will be partially culled. For all other stages, either all individuals present will be removed or none at all.

The general problem formulation in (28) can be extended to allow for controlling whether an immature female is to be reared as surplus or as breeding female replacement. For an immature female, let us suppose that this decision is made when it has survived to the end of the immature stage, denoted by stage subscript i=**1***f* in Figure 6.2. Let s denote the number of immature females surviving to this time point which are to be reared as surplus animals, and consider the following (abridged) transition matrix describing the dynamics of the female part of the herd only:

$$\mathbf{A}=\begin{bmatrix} P_{1f} & 0 & \cdots & \frac{1}{2}f_1 & 0 & \frac{1}{2}f_2 & 0 & 0 \\ 0 & 0 & \cdots & 0 & 0 & 0 & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots & \vdots & \vdots & \vdots \\ \beta_{1f}G_{1f} & 0 & \cdots & 0 & \beta_3 G_3 & 0 & 0 & 0 \\ (1-\beta_{1f})G_{1f} & 0 & \cdots & 0 & P_3+(1-\beta_3)G_3 & 0 & 0 & 0 \\ 0 & 0 & \cdots & \beta_2 p_2 & 0 & 0 & \beta_5 G_5 & 0 \\ 0 & 0 & \cdots & (1-\beta_2)p_2 & 0 & 0 & P_5+(1-\beta_5)G_5 & 0 \\ 0 & 0 & \cdots & 0 & 0 & p_4 & 0 & 0 \end{bmatrix} \tag{30}$$

The second stage (second row and column in **A**) represents the first surplus animal cohort. In contrast to the life-cycle graph in which the parameter σ causes a fixed proportion of stage **1***f* animals to move into stage **2***f*, the structure of transition matrix **A** above is such that there is no pathway into the surplus stage. Let us assume that the transition probability from the juvenile into the first surplus animal stage is the same as that from the juvenile into the first pregnant or barren stage. The matrix element at the intersection of the second row and the first column of **A** in (30), which is equal to zero, would then be replaced by G_{1f}. Then, the following modification of the system dynamics equation (21) introduces the decision to rear a number $s(t)$ of immature females as surplus at time t:

$$n(t+1)=\mathbf{D}\mathbf{A}[n(t)-u(t)+s(t)] \tag{31}$$

where in the present example the diagonal matrix **D** has the form

$$\mathbf{D}=\begin{bmatrix} 1 & 0 & \cdots & 0 & 0 & 0 & 0 & 0 \\ 0 & \dfrac{s}{(n_{1f}-u_{1f}-s)} & \cdots & 0 & 0 & 0 & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \cdots & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & \cdots & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & \cdots & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & \cdots & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & \cdots & 0 & 0 & 0 & 0 & 1 \end{bmatrix} \tag{32}$$

and the vector $s(t)$ has components

$$\begin{aligned} &s^T(t)=\begin{pmatrix}-s & 0 & 0 & 0 & 0 & 0\end{pmatrix} \\ &\text{with} \\ &s\le n_{1f}-u_{1f} \\ &s^T(t)=\text{transpose of vector } s(t) \end{aligned} \tag{33}$$

The structure of matrix **D** and vector $s(t)$ depend on the life-cycle graph and the time point at which the decision to rear immatures as surplus stock is made, and do not need to take on the specific form given here.

The objective function used to evaluate herd productivity is an efficiency ratio, defined as the total gross energy output of the herd devided by its total metabolizable feed energy requirements at the stationary state. Based on equations (15), (18), (19), and (20), the objective function is given by

$$\boldsymbol{I}[\,n(t),u(t),s(t)]=$$

$$\frac{\sum_{i=1}^{h-1} u_i(t)\cdot GE_{EBWT,i} + \sum_{i=1}^{h-1} n_i(t)\cdot GE_{milk,i} + \sum_{i=h+1}^{k} u_i(t)\cdot GE_{EBWT,i}}{\sum_{i=1}^{h-1}\sum_{j} n_i(t)\cdot R_{ij} + \sum_{j} s(t)\cdot R_{hj} + \sum_{i=h+1}^{k}\sum_{j} n_i(t)\cdot R_{ij}} \tag{34}$$

where index values i=1,2,...,h-1 refer to stages other than female surplus stages, i=h indexes the first, and all other values i>h the subsequent female surplus stages. Note that when the optimal solution is such that $s(t)$ is set to zero, all remaining female surplus stages must also have zero abundance in order to satisfy the herd dynamics (31) and steady state (26) equations. To summarize, the herd productivity assessment model can be stated as

$$\underset{u,\,s}{\text{maximize}} \quad \frac{\sum_{i=1}^{h-1} u_i(t)\cdot GE_{EBWT,i} + \sum_{i=1}^{h-1} n_i(t)\cdot GE_{milk,i} + \sum_{i=h+1}^{k} u_i(t)\cdot GE_{EBWT,i}}{\sum_{i=1}^{h-1}\sum_{j} n_i(t)\cdot R_{ij} + \sum_{j} s(t)\cdot R_{hj} + \sum_{i=h+1}^{k}\sum_{j} n_i(t)\cdot R_{ij}}$$

subject to

$$n(t+1)=\mathbf{DA}[\,n(t)-u(t)+s(t)]$$

$$n(t+1)=n(t)$$

$$\sum_{i=1}^{k} n_i(t)=\boldsymbol{c}$$

$$s\le n_{i^*}-u_{i^*}$$

$$0\le u(t)\le n(t) \tag{35}$$

for a production system in which the decision to rear immature females as surplus stock is made at the end of stage i=i^*. Due to the non-linearity of the objective function, this formulation is a non-linear programming problem, which can readily be solved using any standard non-linear programming software. However, problem setup and editing is greatly facilitated when using a spreadsheet software, in combination with a non-linear programming add-in package such as the Premium Solver (Version 2.0, Frontline Systems, Inc., 1996).

The non-negativity constraint on offtake numbers can be relaxed in cases where the dominant eigenvalue of the transition matrix is λ<1, i.e. when the herd is not sustainable due to low survival rates in youngstock or breeding females, and/or insufficient reproductive performance of breeding females. As mentioned before, in these cases the problem (35) cannot be solved. In order to maintain herd size, animals have to be imported, either through purchases or borrowings. In general, herd decline is linked to insufficient availability of breeding female replacements to maintain the size of the mature breeding stock. The non-negativity constraint on offtake numbers can be relaxed to allow for an inflow of female replacements into the herd. In order to account for the capital costs involved, each female replacement animal added to the herd could be valued at the total metabolizable feed energy input required to raise one *surviving* female replacement, based on the following formula:

$$COST_{repl.} = \sum_{i=1}^{s}\sum_{a=1}^{n}\sum_{j}\left[\frac{r_{i,j}(a)}{p_i(a)}\right] \tag{36}$$

where subscript s denotes the stage at the end of which immature females are reared as replacements, and other parameters are defined as in (15).

6.6 Discussion

Herd productivity assessments and energetic efficiency

This work has favoured the use of energetic efficiency as a choice criterion because it provides a common basis on which biological productivity can be assessed and compared among different treatments, management strategies, or among husbandry systems operating in different ecosystems. Clearly, productivity can be measured in many different ways, depending on the type and quantification of input and output flows considered. For purely descriptive purposes, the attractiveness of energetic efficiency stems from its close relationship to the notion of feed conversion efficiency as used in livestock production contexts, as well as from its possible interpretation as a measure of food-chain efficiency (i.e., energy consumption by trophic level n, divided by energy production by trophic level $n-1$), which may be used to identify the physical or biological barriers to higher productivities (Duckham, 1971; Western, 1982). Another advantage is that different livestock products such as meat, milk, and draught power can readily be aggregated in energetic terms, while monetary evaluation of the same products may prove to be difficult when dealing with subsistence producers, or when assigning market prices to livestock products is rendered difficult by the presence of noncompetitive markets. The same is true with respect to important production inputs.

However, an important point to remember is that the use of technical efficiency measures is founded on the notion of certainty and is most often employed in a profit maximizing sense (Anderson et al., 1977). James and Carles (1996) for example explicitly utilize this frame of reference for livestock productivity assessments in arguing that "the most general objective of grazing livestock production, at both farm and national levels, is to obtain maximum economic margin from the available forage resources" (p. 273). Serious doubts may be raised about the general validity of this assumption. Firstly, a characteristic common to all agricultural and livestock production systems, especially when they operate under dryland conditions, is the pervasive influence of stochastic factors on the future state of the system, and thus on outcomes of decisions. In the presence of such uncertainty, available empirical evidence suggests that farmers and livestock producers will tend to be risk averse in making decisions (Anderson and Dillon, 1992). Secondly, in pursuing livestock keeping activities producers may derive other benefits in addition to the production of goods such as meat, milk, draught power and live animals for sale or home consumption. Livestock may also play an important role as a source of financing and insurance, particularly in situations where financial markets are imperfect and opportunities for risk management through formal insurance are not available (Bosman et al., 1997*a*). Hence, when there is considerable uncertainty about the consequences of an action and, at the same time, producers pursue multiple, possibly conflicting goals, it appears to make little sense to assume an unqualified goal of expected profit maximisation (Anderson et al., 1977). Certainly, these considerations will apply to many traditional livestock production systems in developing countries.

In essence, relative to the task of productivity indexing of livestock production systems the important point to be made here is that recommended improvements to existing management practices that aim at increasing livestock productivity must be consistent with the decision-maker's beliefs and preferences. In other words, the most energetically efficient management alternative is not necessarily the one that has also to be preferred by livestock producers. Maximisation of energetic efficiency can help identify the management alternative with the highest biological potential, but this alternative will not necessarily correspond to the choice which maximizes the decision-makers's subjective expected utility. Livestock producers may continually have to trade off the various benefits derived from their herds when making management decisions. For instance, as pointed out by Bosman et al. (1997*a*), insurance and financing goals may induce producers to keep 'unproductive' animals in the herd, thereby reducing biological productivity.

Representation of herd dynamics and derivation of optimal culling regime

The general methodology for assessing biological productivity at the herd level developed in the present work is basically an extension of that proposed by Baptist (1992*b*). While this author assumes that the same inherent survival, fecundity, development rates, as well as yield levels are applied to all breeding and (except, of course, for fecundity rates and milk yields) surplus females alike, the stage-structured population dynamics model employed here is much more flexible since it permits the modelling of life histories in which vital rates and production traits vary with age, stage, or a combination of both factors. Generally, the appropriate definition of relevant life-cycle stages is entirely dependent on the species and on the production context considered. Perhaps most importantly, it has been shown that assessing biological herd productivity can be formalised in a non-linear programming model which determines the optimal stage-specific culling policy that maximizes the chosen biological productivity criterion, subject to the constraints that herd size and structure remain constant. Of course, the choice of the objective criterion to be maximized is not limited to the ecological efficiency index employed here, but could as well be an economic one. For instance, if all

outputs considered were valued in monetary terms, the productivity criterion would represent the economic value of production obtained per unit feed energy input and time (James & Carles, 1996). A major distinction of the proposed methodology compared to other available procedures for the assessment of herd productivity at the steady state of population dynamics resides in the fact that it can readily be used for carrying out a full economic activity analysis of livestock operations. While the computer programs LPEC and PRY mentioned above are fairly flexible with respect to the definition of the productivity criterion, they cannot explicitly take into account the objectives, decision alternatives, technical and resource constraints, as well as managerial limitations that typify the herding enterprise considered.

For comparative studies, the importance of adopting an optimality approach in order to obtain a common basis on which alternatives can be compared with respect to their performance in terms of the chosen productivity criterion must be emphasized. Other authors, such as James and Carles (1996) and Upton (1989, 1993), suggested to use observed or estimated offtake rates for a given management alternative or production system and they did not attempt to simultaneously optimise herd structure and offtake rates with respect to a specific performance criterion. Clearly, a distinction has to be drawn between evaluating potential biological (or economic) productivity, and the level of productivity that can be achieved under the prevailing management practices observed in a specific production system, particularly with respect to offtake rates. Herd productivity is greatly affected by the choice of culling policy, not only directly through the removal of individuals, but also indirectly through its impact on herd structure. Of course, herd management affects herd productivity not only through offtake decisions but, if potential herd productivity is to be assessed, at least this major source of variation should be controlled for in comparative assessments. Productivity assessments may be biased downwards if they are based on observed or estimated, suboptimal offtake decisions. An additional motivation to use an optimality approach to determine optimal culling policy and herd structure stems from the fact that accurate data on offtake rates by animal category and time unit are generally difficult to obtain in production system studies.

Although the relevance of selective culling rates for the determination of productivity levels in livestock herds has clearly been recognised by Baptist (1992b: 265), his simulation approach based on life tables brakes down with respect to the identification of optimal culling policies for breeding females, because “too many combinations of different ages are possible”. Indeed, the different ways in which herd composition can be changed is virtually infinite and therefore all possible strategies cannot be compared using simulation runs. Whenever a key measure of economic or biological performance can be nominated, applying an optimisation algorithm is a far more powerful approach that enables the optimal policy to be precisely calculated. Note that the general type of linear control system formulation for multi-cohort herds adopted in this work has previously also been proposed by Upton (1989). Surprisingly, however, he did not envisage to apply an optimisation algorithm for the simultaneous derivation of the optimal steady state culling policy and herd structure. Similarly to the above cited statement made by Baptist, he argued that the principle difficulty resides in the fact that there are too many different possible combinations of herd structures and offtake rates that need to be compared, and concluded that "selection of a particular solution is a question of judgement" (Upton, 1989:161). The present work has shown that more rigorous methods are available to circumvent this problem.

Alternative model parameterisations

In the example used to illustrate the developed herd productivity assessment procedure, it was assumed that the hypothetical livestock herd is of the birth pulse type, i.e. that reproduction is concentrated in a short breeding season. This requires specific approximations for model parameters which may not hold for continuously reproducing livestock species or aseasonally managed livestock herds. Caswell (1989) gives approximations for birth-flow survival probabilities and fertilities. Alternatively, continuous reproduction in domestic livestock herds can be accomodated for by making appropriate changes to the corrresponding life-cycle graph, based on the following reasoning. The major difference between an aseasonal and a seasonal breeding regime resides in the length of the time interval between successive mating events. Whereas in its simplest from controlled breeding logically implies a one year breeding interval and thus a fixed time period between successive mating events, this parameter may vary considerably under unrestricted breeding. It follows that in the aseasonal case birth intervals are a function of both the probability of conception and the timespan between consecutive mating events. For fertile breeding females the latter parameter determines when, on average, the first postpartum service occurs. It also determines the average waiting time until next service for breeding females that failed to conceive.

In general, the shortest period from birth to conception corresponds to the time until occurrence of the first oestrus postpartum. Expected birth intervals for various combinations of values for species specific conception rate and period between successive matings can be calculated in order to identify a reasonable value for the latter parameter. The following formula can be used to estimate average birth intervals (T_b)

based on conception rate (β), gestation period (T_g), and period between successive mating events (T_m):

$$T_b = \beta (T_g + T_m) + \sum_{n=1}^{\infty} \beta (1 - \beta)^n (T_g + n \cdot T_m) \quad (37)$$

where n denotes the projection time step. It is assumed here that all parameters are population averages and remain constant over time. Depending on the determined value of T_b, a projection time step of less than the length of the gestation period may be required to model the dynamics of the livestock species of interest. While the general methodology does not impose any restrictions in this respect, such a choice may cause a significant increase in model complexity in terms of the number of different stages and associated model parameters that need to be estimated.

The second important assumption that was made in this work concerns the duration of individual stages in the life cycle, which affects the way stage transition probabilities are approximated. Stage duration was assumed to be fixed, and situations may arise where this assumption is considered inappropriate for an accurate representation of population dynamics. Several alternative approximations for stage transition probabilities, which depend on the within-stage age distribution and the distribution of stage durations among individuals, were presented by Caswell (1989).

Sensitivity analysis

A valuable feature of the procedure for productivity indexing employed in this work is the possibility of conducting sensitivity analyses. Sensitivity analysis serves two main purposes. Firstly, as tools for model assessment sensitivity calculations may help in identifying critical components of a model and can be used for model validation. Generally, particular emphasis should be given to the appropriate specification of critical parts of the model structure and to accurately estimating parameters to which model results are very sensitive. Secondly, sensitivity analyses are important management tools which can help to indicate the type of controls that should be applied in order to most efficiently bring about desired changes in system response.

In the present setting sensitivity analyses can be carried out in two different ways. One possibility is to conduct a sensitivity analysis within the non-linear programming framework. Here, the most basic form of sensitivity analysis information is provided by the dual values or shadow prices of binding constraints, but these are of little interest in situations where only steady state constraints with respect to herd size and structure are included in the optimization models studied. However, sensitivity of model results to individual parameters can be checked by rerunning the original model consecutively after gradual changes in a single parameter have been made over some reasonable range. Simultaneous changes in several exogenous model parameters such as mortality, fecundity, and developmental rates can also be investigated through parametric programming (Hillier and Lieberman, 1986).

Alternatively, one can conduct asymtpotic analyses on the transition matrix for the female part of a livestock herd and investigate its long-term dynamics. Because the dominant eigenvalue, λ, and the rigth and left eigenvectors, *w* and *v*, are properties of the matrix entries (i.e., reproductive, survival, and developmental rates) rather than initial conditions, they can be used as demographic statistics. The computation of eigenvalue sensitivities and elasticities pertains to perturbation analysis, a special form of sensitivity analysis that examines the impact of changes in vital rates on asymptotic population growth. In livestock herds, the asymptotic growth rate determines potential offtake rates and therefore is an important variable affecting overall biological herd productivity. An important advantage of elasticities of λ with respect to individual matrix entries is that they sum to one and thus can help to identify those vital rates to which λ is most sensitive. For instance, this is a property that is not shared by sensitivity analyses carried out through parametric programming. Elasticities can also be calculated with respect to parameters other than matrix entries themselves, but in this case they also do not sum to one and cannot be interpreted as contributions to asymptotic population growth rate. Note that the interpretation and utilization of eigenvalue elasticities in matrix population models is analogous to the concept of elasticity as used in microeconomic theory. Using matrix algebra, eigenvalue elasticities are easy to calculate once the eigenvectors of the projection matrix are known (Caswell, 1996*b*). Cochran and Ellner (1992) have made available a FORTRAN 77 program which calculates a number of measures for the analysis of population projection matrices, including the complete eigenvalue spectrum as well as other, age-based life history parameters. The same authors also suggested the use of bootstrapping methods to make rigourous statistical comparisons of these parameters.

To summarize, the information that can be derived from a stage-based demographic description using matrix population models appears to be much richer than that usually obtained from conventional sensitivity analyses such as those proposed by Peacock (1987) or Upton (1985, 1989). The latter authors proposed to separately vary (vital) parameters by one standard error and to investigate the effect of such a change on

outcomes of interest. This, however, is a rather large change in parameter values. In order to be valid the entire approach must be based on the unrealistic assumption that all model parameters are independent from each other. In contrast, the concept of eigenvalue sensitivity is based on infinitessimal parameter alterations, and under these conditions the independence assumption is much less likely to be violated.

6.7 Conclusions

The approach to steady state herd productivity assessment proposed in this work is very general and can easily be applied to a wide range of domestic livestock species and production systems. Stage-structured matrix population models can be generalized to complex life cycles in which individual animals can be classified by several factors other than age. The proposed method represents a readily accessible tool for constructing and analysing herd dynamics models that reflect important biological factors determining survival and reproductive rates in domestic livestock species. In many situations, these vital rates depend on size, developmental, or reproductive stage much more than on age. The use of stage-structured matrix population models in conjunction with non-linear programming for the derivation of the optimal steady state herd structure and culling policy removes most limitations of previously published procedures for steady state herd productivity assessment. This includes the possibility of taking into account stage-dependent vital rates and production performances, and the determination of optimal yield- and stage-specific selective culling rates. Compared to the work of James and Carles (1996) and that of Baptist (1992*a*), an attractive feature of the proposed optimality approach to steady state herd productivity assessment is that it reduces the influence of subjective judgements on model results, an element which certainly is involved when using heuristic culling rules, or observed or estimated offtake rates. Furthermore, the entire procedure is easily implemented in any standard commercially available spreadsheet program. The only specialized software required is a non-linear programming add-in package for solving the optimisation model.

Chapter 7

Assessing the effect of controlled seasonal breeding on steady state productivity of pastoral goat herds in northern Kenya

7.1 Introduction

A major constraint on biological productivity of grazing livestock under semi-arid conditions in northern Kenya is the marked seasonal fluctuations in the availability and quality of rangeland resources (Schwartz & Schwartz, 1985). With the increasing trend towards sedentarization of pastoral herds and households, the search for an alternative to herd mobility as the most effective adaptive management strategy to attenuate the effects of seasonality in production resources is an issue of growing concern (Roth, 1995). Continuous breeding throughout the year, which is made possible due to the non-seasonal reproductive behaviour of local goat breeds, is typical for pastoral goat flocks in northern Kenya. However, this strategy tends to produce poor survival as well as reproductive and productive performances whenever late pregnancy and birth fall into periods with suboptimal forage availability (Wilson et al., 1985; Delgadillo & Malpaux, 1996; Mellado, et al., 1996; Walkden-Brown & Restall, 1996). In general, an aseasonal breeding regime implies that nutrient requirements of the flock remain relatively constant over the year. With the transition of pastoral households and their herds to sedentism, a significant increase in the likelihood of the occurrence of serious imbalances between peak nutritional requirements of livestock herds and seasonal feed supplies can be expected.

The results of an experimental study conducted in northern Kenya on the effects of controlled seasonal breeding on biological performance traits of pastoral goat herds has revealed that such a management practice could effectively reduce the impact of fluctuations in nutrient supply on youngstock survival, mainly through concomitant improvements in birth weights and milk production of dams (Chapters 3 and 5). In contrast, the effects on reproductive and growth performance were less clear-cut (Chapters 2 and 4). As a synthesis of the previous results, the present chapter is concerned with the assessment and comparison of overall biological herd productivity achieved in goat herds subjected to controlled breeding at different time points in a year. The first hypothesis for testing is that there is an optimal period in a year to which breeding can be restricted to improve overall biological productivity of goat flocks. Secondly, a simulated, aseasonally reproducing herd is used as a reference in testing whether controlled breeding in goat herds is superior to uncontrolled breeding under semi-arid rangeland conditions in northern Kenya. Thirdly, the question of whether a restricted, once-a-year breeding regime entails a significant increase in production risk is addressed. In addition, hypothesis testing is carried out in relation to two different levels of milk extraction for human consumption. It is important to take such variations in production goals into account because, traditionally, goats play a crucial role in buffering insecurities and imbalances in food supply to pastoral households and are reared for dual-purpose meat and milk production, while the transition towards a more sedentary life-style increases the pressure on pastoral producers to specialise and commercialise their mode of production.

Productivity assessments are made using a newly developed approach to steady state herd productivity assessment (Chapter, 6). The procedure is based on a stage-based description of population dynamics and uses non-linear programming to derive the steady state herd structure and culling policy that maximizes overall energetic efficiency of pastoral goatkeeping. The efficiency of energy transformation (in percent), which has also been called ecological efficiency by Coughenour et al. (1985), from metabolizable feed energy into gross energy available for human consumption is a relevant performance index under the assumption that feed is the main limiting resource for grazing livestock production (James and Carles, 1992). Also, using gross dietary yield as an aggregate measure of output, instead of production or economic margin measured in monetary terms, is probably more appropriate in situations where profit maximisation cannot be assumed to be the primary objective of the decision maker. This is often the case in traditional, subsistence oriented pastoral production systems (Behnke, 1985; Upton, 1989).

7.2 Materials and Methods

Experimental data

Data for the parameterisation of the herd productivity assessment models studied in this work were obtained from the results of an experiment conducted between January 1984 and January 1988 at the Ngare Ndare Research Station of the University of Nairobi in Isiolo District, northern Kenya. The experimental design and herd management were described in detail in Chapter 1. The experiment consisted of 145 does of the SEA type, which were maintained under simulated pastoral management conditions and used for a total of 381 exposures. These were distributed among 18 consecutive breeding groups consisting of approximately 18 does each. Year-round mating, kidding, and weaning was achieved by consecutively introducing a buck into each of the 18 breeding groups for a period of two months duration. 381 kids were born during the experiment, and weaning occurred at 16 weeks of age. Three complete production cycles, ranging from mating until the time at which youngstock had reached an age of two years were obtained for five of the six consecutive two-month breeding periods per year generated by the experiment. Due to incomplete records for the third repetition of the sixth mating period, which was initiated in December 1986, only two complete cycles were available for this period. The experimental treatment thus consisted of six different mating periods or seasons, the first taking place from February to March (labelled as mating season 1) and the sixth taking place from December to January (mating season 6). Mating seasons 4 and 5 (August to October, and October to December) had to be assumed to have taken place over a period of three months due to a delay of one month which occurred in setting up the first group of mating season 4 in 1984.

Statistical analyses were carried out on all traits required to parameterise the herd productivity assessment models for each of the six mating seasons (see section *model parameterisation and description of scenarios performed*). For details on the statistical modelling procedures employed, reference is made to Chapters 2 through 5. However, an important point to note here is that the adoption of longitudinal data analysis methods is crucial in order to obtain reliable estimates of survival rates, of liveweight growth and development over time, as well as of lactational milk yields.

A matrix population model for pastoral goat herds

The principles outlined in Chapter 6 were utilized to formulate a population dynamics model for pastoral goat herds. The model describes the dynamics of a herd of breeding females and their female and male offspring. Male breeding animals are not considered explicitly, and it is assumed that their abundance at any time is sufficiently high so as not to limit reproduction. Thus, all male offspring produced are expected to be reared as surplus animals. The model also allows for rearing immature females as surplus animals which are culled at an appropriate age, instead of using them as breeding female replacements. The decision as to whether an immature female is to be reared as female replacement or surplus stock was supposed to take place at the age of 10 months. Births are assumed to occur at one point during the projection time interval so that the herd is of the birth pulse type. Finally, it is supposed that within each time interval the population is censused immediately after reproduction.

The model was intended to be amenable to both the analytical methods for matrix population models, and to assessments of herd productivity using mathematical programming techniques (Chapter 6). The former requires the transition matrix to be irreducible, whereas the latter does not. As discussed in Caswell (1989, 1996b), a reducible transition matrix contains at least one stage that cannot contribute, by any development path, to some other stages. For instance, this occurs with the non-reproducing or surplus male and female parts of the population which form sequences of stages with only one-way communication, i.e. there is no pathway back to the part of the life cycle that does reproduce. Therefore, the surplus stages of both sexes were omitted from the productivity assessment model for carrying out matrix analyses. This, however, does not affect or invalidate the analytical results obtained, since, in the present context, the dynamics of the breeding herd are independent of those of surplus animals.

The life cycle graph describing the dynamics of the breeding female portion of the herd is shown in Figure 7.1. The projection interval from [t, t+1] is five months and approximates the gestation period for goats reported in the literature (e.g., Devendra and Burns, 1983). The population is divided into two immature stages (birth to 5, and 5 to 10 months of age), one replacement stage, and a total of 38 breeding female stages. The latter are structured according to the reproductive status (pregnant, non-pregnant, lactating) and the parity number of breeding does. It takes one year to complete a full reproductive cycle, which is split up into pregnancy and lactation stages for fertile does, and two consecutive non-pregnant stages for temporarily infertile animals. It is assumed that mating occurs once a year and is concentrated in a short breeding season. The self-loops attached to the lactation and some of the non-pregnant stages indicate that the duration of these stages exceeds the 5 months projection interval. Stage durations are fixed for all stages. Coefficients

labelling arcs in Figure 7.1 specify the recruitment rates into each of the i stages. The β_i, P_i, and G_i parameters denote, respectively, stage-specific marginal probabilities of conception, surviving and remaining in the same stage, or of surviving and growing into one of the next stages. The parameters p_i are stage-specific probabilities of survival over one time interval; the f_i's represent stage-specific fecundity rates. The subscripts $np(k, l)$ for non-pregnant stages identify the kth non-pregnant stage for an animal of parity l.

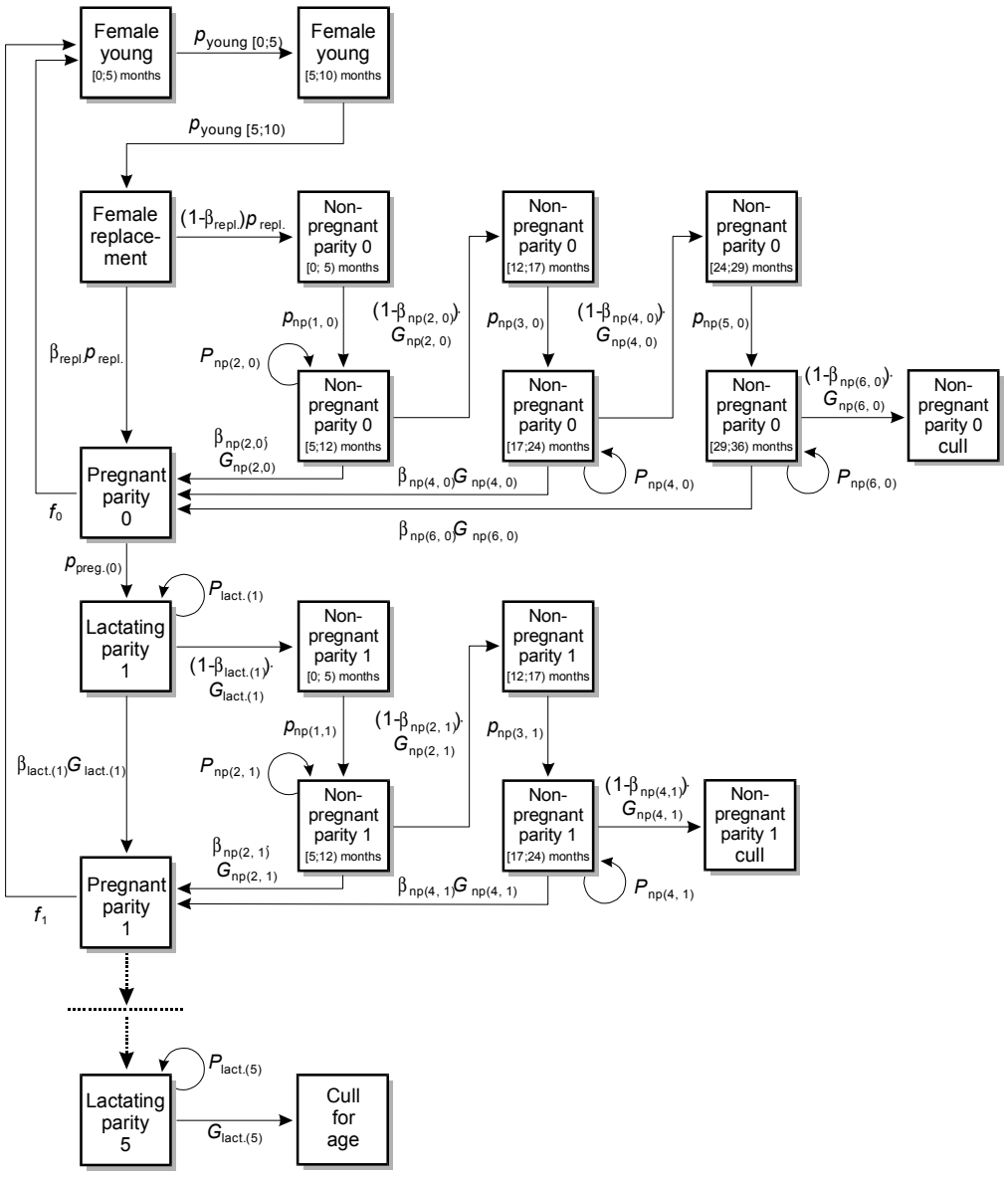

Figure 7.1. Life cycle graph for breeding does. The reproductive cycles for does in parities 2, 3 and 4 are identical to the one depicted for primiparous does. Surviving breeding does are culled (or die) after completing the fifth lactation.

The life history of a breeding female begins with its birth into the juvenile stage (0 to 5 months of age), then it either dies or becomes a weaned female young five months later. The decision to rear an animal as a breeding female replacement or as surplus is made at ten months of age. First mating occurs at the age of fifteen months or approximately 65 weeks. This is in agreement with the average age at first breeding of 67.8 weeks (±12.6) observed during the experiment.

The parity number of does is increased by one whenever a pregnant doe survives until parturition. A fertile doe completes a full reproductive cycle at the end of the seventh lactation month, i.e. at the beginning of the next breeding season, which is also the onset of a new reproductive cycle. Breeding does which were mated for the first time in their parity class and failed to conceive move through two non-pregnant stages (0 to 5 months and 5 to 12 months) and are rebred the following year. If they again fail to conceive, the process is

repeated for an additional year (12 to 17 and 17 to 24 months non-pregnant). Nulliparous females are allowed to remain reproductively inactive for a maximum of 36 months, and are culled (or die) if no pregnancy is detected at the end of the third consecutive infertile cycle. The infertile state for breeding females of parity ≥ 1 is limited to two consecutive cycles, or a maximum period of two years. Principally, it is straightforward to extend the time period potentially spent by an animal as reproductively inactive by simply adding further non-pregnant stages to the life cycle graph. However, the associated increases in model size and data requirements are hardly justified if, as it is the case in pastoral goat herds, the rate of non-conceivers is of the order of 5-15%, such that very few animals remain infertile after three unsuccessful consecutive matings (e.g., 0.34% if 15% of all animals present at mating fail to conceive).

The cull for age threshold was set to the period after completion of the fifth lactation, both for computational and data analysis reasons. The decision to ignore breeding female stage classes beyond the fifth parity was supported by the fact that only 5 out of the 287 fertilisations in the experiment occurred the fifth or higher parity stage. Similar reproductive life-spans of SEA goats have been reported by Peacock (1984) and Wilson (1992).

The life cycle graph in Figure 7.1 was used to model each of the six different mating season groups of the experiment. The experimental design did not include an "aseasonal" control group to which the restricted breeding regimes could have been compared. However, the matrix population modelling technique offered the opportunity to at least approximate such a breeding strategy by suitably modifying the life cycle graph in Figure 7.1. The construction of the life-cycle graph of an aseasonally managed pastoral goat herd was based on the reasoning discussed in Chapter 6. There, it was argued that the major difference between aseasonal and seasonal breeding regimes resides in the length of the time interval between successive mating events, and that in the aseasonal case kidding intervals are a function of both the probability of conception and the timespan between consecutive mating events. In goats, the shortest period from kidding to conception corresponds to the time until occurrence of the first oestrus postpartum, which implies a minimum kidding interval of about 175 days (Devendra and Burns, 1983). Wilson (1992) reported mean kidding intervals for goats of the SEA type of 306 days (Maasai), 297 days (Mubende), 233 days (Mashona) and 14 months (Boran).

Table 7.1. Estimated kidding intervals (days) for different values of conception rate and period between successive mating events. Calculations are based on equation (37) of Chapter 6.

	Period between successive mating events in days						
Conception rate	61	91	122	152	183	213	241
0.99	214	244	275	306	336	367	398
0.95	216	248	280	312	344	376	407
0.90	220	253	287	321	355	389	419
0.85	224	259	295	331	367	403	433
0.80	228	266	304	342	380	418	449

Using equation (37) of Chapter 6, expected kidding intervals for various combinations of values for conception rate and period between successive matings were calculated in order to identify a reasonable value for the average period between successive mating events. The figures in Table 7.1 suggest that an average period between successive mating events of about 122 to 152 days returns estimates of kidding intervals which compare fairly well with the range reported by Wilson (1992). A period of 152 days or roughly five months was finally chosen for modelling the aseasonal breeding regime. The main reason for this was that selecting a shorter time period would have resulted in a projection time step less than five months, and thus in a more complicated model structure of the model due to the corresponding increase in the number of stages. An average period of five months between successive matings leads to the life cycle graph shown in Figure 7.2. Note that all self-loops vanish, since the period between successive mating events is equal to the projection time step. Conditioned upon survival, non-pregnant does breed on average every fifth month, and the first postpartum service for fertile does occurs after the fifth month of lactation. The number of non-pregnant stages by parity class is the same as for the seasonal breeding life cycle, although the maximum duration of reproductive inactivity is reduced to 30 (parity 0) and 20 months (parity ≥ 1). The population dynamics of the surplus female and male portions of a herd were modelled according to a simple age-structured life cycle (Figure 7.3). The life history is identical for both breeding regimes. Surplus animals are kept in the herd until they reach a maximum age of 35 months, after which they are culled. The p_i coefficients labelling arcs denote age-/sex-specific survival probabilites over a five month time interval.

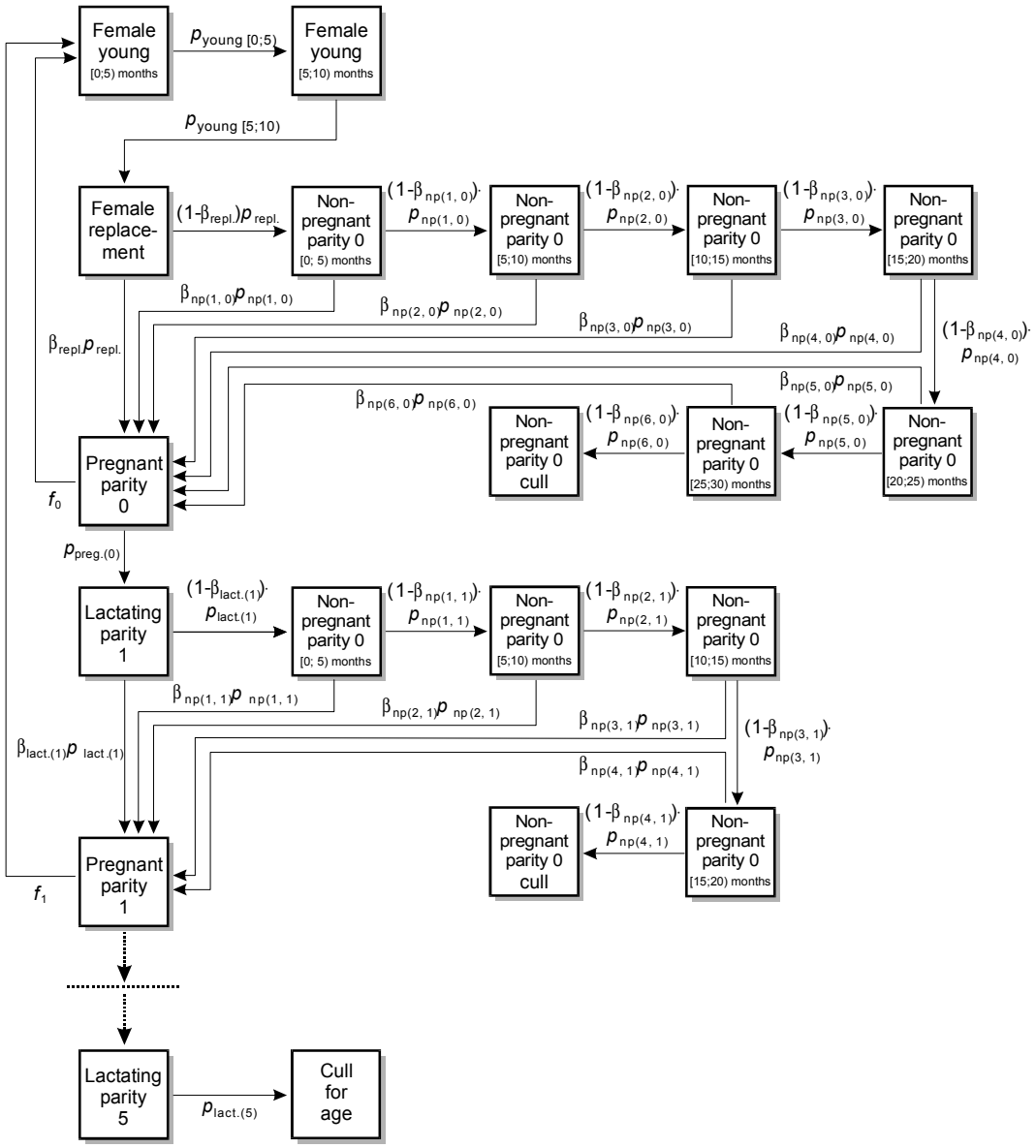

Figure 7.2. Life cycle graph for breeding does, aseasonal breeding regime.

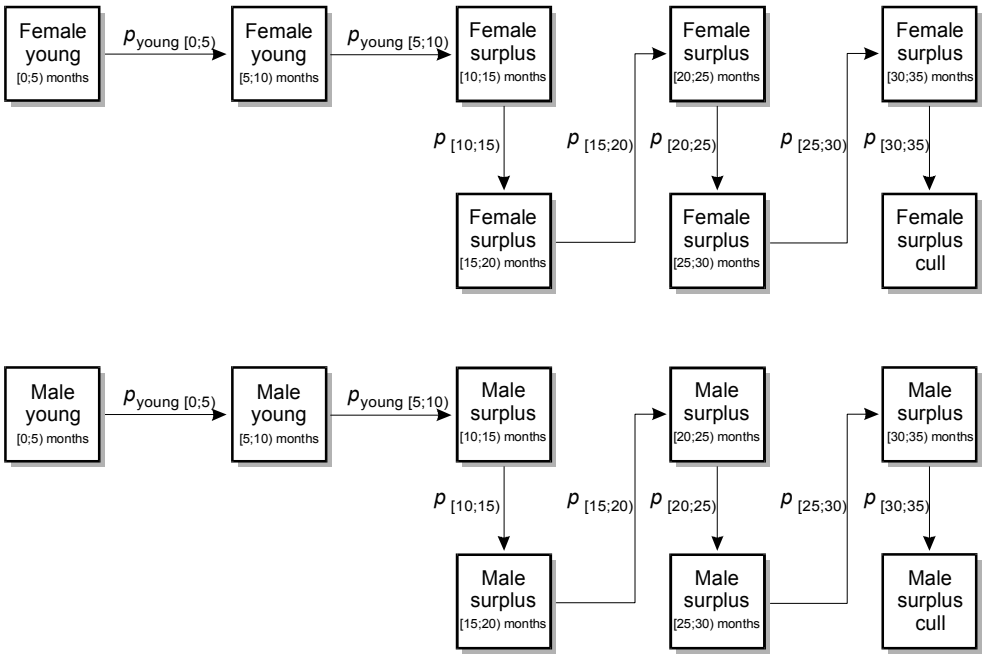

Figure 7.3. Life cycle graphs for surplus animals.

Estimation of feed energy inputs

Metabolizable energy (ME) requirements were assessed according to the factorial method, in which requirements for maintenance, growth, pregnancy, and lactation are estimated separately, and then summed to give the total net requirement (ARC, 1980). Values of daily ME requirements for maintenance, growth, pregnancy, and lactation were based on those recommended for goats by NRC (1981). A 50 percent increment was applied to the basic maintenance requirements of animals older than 16 weeks of age, as suggested by NRC for medium activity levels under grazing conditions on semi-arid, slightly hilly rangeland pastures. Information on weight development, weight gain, and lactation yield in all life cycle stages were obtained from growth and lactation curves that were fitted to experimental data (Chapters 4 and 5).

Recall that in modelling herd growth, a postbreeding census was assumed, and therefore projected stage abundances refer to those observed at time t in each time interval $[t, t+1]$. Consequently, an account is taken of the fact that individuals present at the beginning of a time interval survive until its end. ME requirements per animal over a single time interval were therefore corrected for mortality. Given that longitudinal stage-specific survival data were available, it was possible to estimate survival curves for each life history stage. Then, an appropriate assessment of stage-specific ME requirements for each body function over the interval $[t, t+1]$ would have consisted in summing together the *daily* requirements for each body function for all days a within $[t, t+1]$, weighted by the probability of surviving until the end of day a. However, to reduce the amount of calculation involved, it was decided to divide the five months (or roughly 152 days) projection time interval into intervals of length l=14 days (breeding female stages) and l=56 days (youngstock, replacement, and surplus animal stages).

With repect to energy requirements for pregnancy, the approach suggested by NRC (1981) was adopted, which is to increase daily ME requirements per animal by a fixed value of 5.94 MJ during the last two months of pregnancy. Energy released from mobilization of body reserves was also taken into account in calculating total ME requirements for each life history stage. Substantial weight losses usually occur soon after parturition, but are also common in situations of low or declining quantity and quality of forage on offer. For time periods during which animals were losing weight, the energy released from body reserves and used to meet maintenance, pregnancy, and/or lactation requirements was estimated as follows.

Body tissue was assumed to have an energy content of 20 MJ/kg, with a coefficient of conversion to net energy (NE) of 0.82 (Konandreas and Anderson, 1982). Based on these assumptions, net energy available per kg body tissue mobilized was approximately 16.4 MJ. Upon making the additional assumption that the average efficiency of conversion of feed-ME into NE is 0.56, the amount of feed-ME replaced per kg body tissue mobilized was equal to 29.3 MJ ME. Whenever animals were losing weight, this value was used to replace ME requirements for growth. Negative growth rates thus effectively reduced the total amount of ME

from feed resources that must have been available to cover observed maintenance, pregnancy, and/or lactation requirements. Based on a similar reasoning, the expected amount of energy available to kids from milk consumed until weaning was accounted for in calculating total metabolizable feed energy requirements per kid present at the beginning of the youngstock stage (0 to 5 months). The expected milk produced by lactating does until weaning was estimated from stage-specific lactation curves and survival rates of does until weaning. From these estimates, the amount of milk extracted for milk yield measurements during the experiment had to be substracted. Since milk yield measurements were made once every 14 days and implied complete removal of a day's yield, the average experimental milk offtake was about 1/14th of total milk produced until weaning. The procedure employed to calculate expected gross energy yields from milk produced is described in the next section. Conversion of gross energy content into ME content per kg milk was performed using a digestibility coefficient of 0.93.

Estimation of herd outputs

Herd output was defined in terms of total meat and milk offtakes for human consumption per projection time interval, valued at their gross energy contents. The quantity of milk extracted for human consumption over one projection time step was assumed to correspond to a fixed proportion of expected total milk produced by animals in lactation stages (see the section on *model parameterisation and description of scenarios performed* further below).

For each life cycle stage, body weight estimates for animals present at the beginning of each time step were available from corresponding stage-specific growth curves (Chapter 4). The main problem resided in estimating the gross energy content per kg of empty body and carcass weight in different life cycle stages. Information on this subject is very scarce for tropical goat breeds in general, and are virtually nonexistent for goats of the SEA type. Most of the published experiments relate to temperate breeds (e.g., Panaretto, 1963; Jagush et al., 1983; Brown and Taylor, 1985; Sanz Sampelayo et al., 1990; Benjamin et al., 1993). The few examples on tropical breeds that could be found were those of Gosh and Moitra (1992) on Black Bengal goats, Aganda et al. (1989) on Sahel and Maradi goats, and Viljoen et al. (1988) on Boer goats. The last study analysed body composition of does over a relatively wide range of ages and live masses for does, and the results reported therein are used here as a basis to estimate gross energy contents per kg of empty body and carcass weight in different life cycle stages.

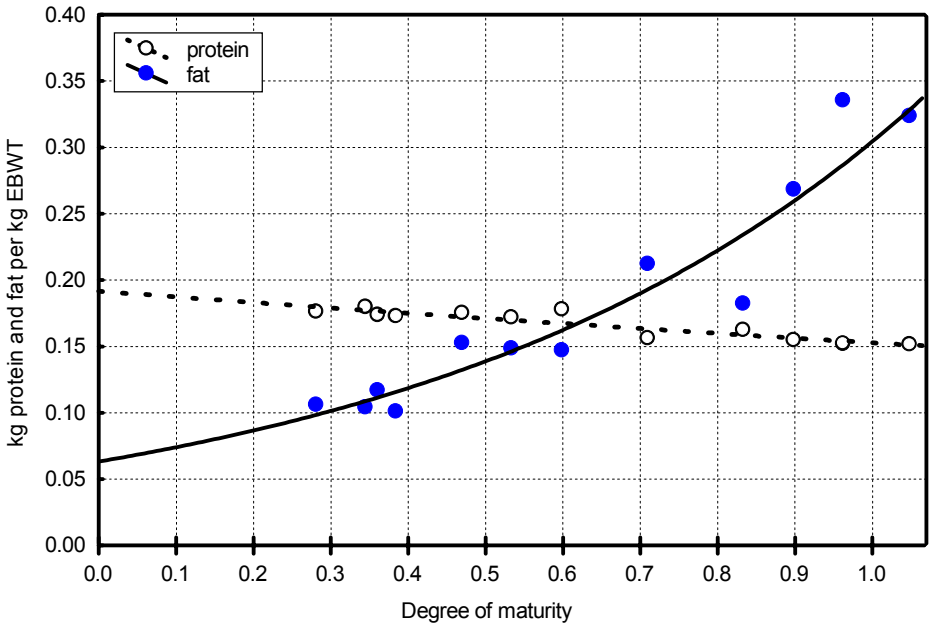

Figure 7.4. Relationships between degree of maturity and protein and fat contents in empty bodies of goats (data from Viljoen et al., 1988).

In their paper, Viljoen et al. provided data on age, live masses, carcass analysis, and gut contents of 12 Boer goat does. Live masses ranged between 20 and 60 kg, and ages between 7 and 44 months. The amounts of body protein and fat measured on the 12 experimental animals given in this paper were re-expressed as a

function of the degree of maturity, assuming that the mature live weight in the population of Boer goat does from which the experimental animals were sampled was approximately 60 kg. This corresponds to the lower limit of the range of mature live weights (60 to 75 kg) reported by Devendra and Burns (1983) for female Boer goats. Average empty body weight in the experiment published by Viljoen et al. was 84% of live mass, and thus an empty body weight at maturity of 50 kg was assumed. After expressing all measured empty body weights relative to the empty weight of mature animals, the following regressions were fitted to data on proportions of protein and fat contained in empty live masses:

$$\log[\ PFAT\ ] = -2.760\,(\ SE\ 0.095\ ) + 1.571\,(\ SE\ 0.141\ ) \cdot [\ DMATURITY\ ]$$
$$R^2 = 0.93 \quad F(1,10) = 123.56$$

$$\log[\ PPROTEIN\ ] = -1.652\,(\ SE\ 0.022\ ) - 0.226\,(\ SE\ 0.033\ ) \cdot [\ DMATURITY\ ]$$
$$R^2 = 0.83 \quad F(1,10) = 48.14$$

Figure 7.4 gives a plot of the relationships between degree of maturity and proportions of protein and fat per unit empty body weight. For instance, protein and fat contents in empty body at maturity were estimated as 15.3 and 30.4 percent, respectively. In the absence of any further information, the above relationships were assumed to hold true for both female and male animals.

Data on empty body and carcass weights for SEA goats were available from an experiment conducted simultaneously to the present study at the Ngare Ndare research station (Hofman an Schwartz, 1987). From these data, average empty body weight was estimated as 82.0 percent (SD 4.35, N=48 goats) of live mass, and dressed carcass weight as 59.6 percent (SD 5.15, N=48 goats) of empty body weight. No significant differences were found between female and male animals. The live weight of mature SEA goats was assumed to be 38 and 48 kg (31.1 and 39.3 kg empty body weight) for females and males, respectively. Then, based on a gross energetic value for protein (GE_P) and fat (GE_F) of, respectively, 38.12 MJ/kg and 24.52 MJ/kg (Zygoyiannis and Katsaounis, 1986), gross energy yield per live animal offtake in stage *i* was calculated as

$$GE_{EBWT,i} = PPFAT_i \cdot EBWT_i \cdot GE_F + PPROTEIN_i \cdot EBWT_i \cdot GE_P$$

$$GE_{carcass,i} = 0.596 \cdot GE_{EBWT,i}$$

where

$EBWT_i$ = is the empty body weight of an animal at the beginning of stage *i.*
$GE_{EBWT,i}$ = is the gross energy yield in empty body per live animal offtake in stage *i.*
$GE_{carcass,i}$ = is the gross energy yield in dressed carcass per live animal offtake in stage *i.*
$PPFAT_i$ = is the proportional fat content per kg $EBWT_i$, obtained from equation (44) upon expressing $EBWT_i$ in terms of degree of maturity.
$PPROTEIN_i$ = is the proportional protein content per kg $EBWT_i$, obtained from equation (45) upon expressing $EBWT_i$ in terms of degree of maturity.

Whenever average empty body weight at entry into a stage class exceeded the assumed weight at maturity, degree of maturity was set to 1 in calculating gross energy yields.

Similarly to the assessment of energy requirements, milk yield and milk offtake per animal present at the start of a time interval [*t*, *t*+1] in lactation stage *i* was adjusted for mortality. Goat milk was assumed to contain 4.48 g/kg fat, 3.65 g/kg protein, and 5.02 g/kg lactose, giving a total dry matter content of 13.15 g/kg milk (Jagush et al., 1983). Using the energetic values for protein and fat given above, and an energetic value of lactose of 16.54 MJ/kg, results in a gross energy content of milk (GE_m) of 3.43 MJ/kg.

Model parameterisation and description of scenarios performed

As mentioned above, the parameterisation of the individual herd productivity assessment models was based on results of statistical analyses of experimental data obtained on stage-specific conception, fecundity and survival rates, as well as on liveweight development and milk yields in each of the six different mating season groups. Since the ultimate objective of the productivity assessment exercise was to evaluate differences in energetic efficiency achieved under each of these treatments, some form of statistical

significance test was required. This, of course, presupposed that more than one observation in each treatment group was available. Fortunately, as indicated above all mating season groups were observed over three consecutive production cycles, except for mating season six, which had only two replications. The procedure then involved obtaining estimates by mating season group *and* production cycle for each parameter. Several of the statistical models used were of the mixed model type, with production cycle being treated as a random effect, so that these estimates implied a narrow inference space. However, for all parameters, mean values by mating season group, but averaged over production cycles, were also estimated. These were used to construct an "average" model for each mating season group, on which some of the matrix analyses were performed. In sum, a total of 23 different herd productivity models were parameterised in this way.

Parameterisation of the aseasonal reference model was accomplished by fitting the same type of models as above, but excluding the mating season treatment effect. Parameter values for the aseasonal model thus correspond to expectations obtained by treating the experimental data set as if no restriction on the timing of breeding had been implemented throughout the year. Four different aseasonal herd productivity models were constructed; one model for each production cycle, and, as for the mating season groups, an additional "average" model that combines the information from all three production cycles.

Parity-specific estimates of survival rates, body weights, and milk yields of does were only available up to parity class four. Because very few animals lactated more than four times during the experiment, observations of such animals were pooled with those of parity stage four animals. Consequently, parameter values for parity class five in the life cycle graphs (Figures 7.2 and 7.3) were identical to those for parity class four.

Two different types of scenarios were investigated with respect to milk offtake rates. In baseline model runs, milk offtake corresponded to the amount extracted for milk yield measurements during the experiment, or roughly 1/14th of total milk produced in each lactation stage. Pastoral goat herds are generally reared as dual purpose meat and milk herds, and milk offtake rates for human consumption affect both survival and growth rates of kids.

Based on the assumption that the dual purpose mode of production would affect the relative ranking of mating seasons with respect to productive efficiency, a scenario with increased milk offtake for human consumption was designed. No information on milk offtake rates per lactation in pastoral goat herds in Kenya was available, and use was made of an expert opinion. H.J. Schwartz (personal communication) suggested that roughly one third of total lactational milk yield could be considered as an upper limit for milk offtake rates in pastoral goat herds. Thus, in the increased milk offtake scenario an offtake rate for human consumption of 33 percent (including the experimental offtake) of all milk produced by does in the different parity stage classes was assumed.

All parameter values in herd productivity models for the increased milk offtake scenario were the same as those for the baseline scenario, except for those relating to kid survival and body weight development. Milk yield of does until weaning, categorized into five classes (10 kg apart), was one of the predictor variables used in the statistical analysis for estimating these two traits. Therefore, using appropriate estimable functions of the fixed effects (i.e., linear combinations of the model parameters), it was possible to estimate kid survival probabilities and body weights for reduced milk availability until weaning. To accomplish this, estimated mean milk yields in each of the mating season groups and the aseasonal control were used as a reference from which the 67 percent yield levels were computed. Next, interpolation weights between lower and upper class midpoints of the reduced yield classes were calculated; these were then used as coefficients for the levels of the milk yield fixed effect in estimable functions. A total of 27 additional (including the aseasonal control group) runs of the herd productivity model were required to obtain the results of the increased milk offtake scenario.

In order to avoid problems relating to demographic stochasticity, all model runs were performed using a steady state herd size of c=10.000 animals in equation (27) of Chapter 6. For both scenarios, energetic efficiency as defined in Chapter 6 was used as the objective criterion to be maximized. Two additional productivity indices were computed from the solution of the non-linear programming model. These were a reproductive performance (*RPI*) and flock productivity (*FPI*) index, similar to those reported by Bosman et al. (1997):

$$RPI = \frac{n_{\text{young}[5;10)}(t) \cdot EBWT_{\text{young}[5;10)}}{\sum_i n_i(t)}$$

where

RPI = is the reproductive performance in terms of weaned empty body weight

(kg) per doe and five months time unit at the stationary state.

$n_{\text{young [5;10)}}$ = is the number of animals present in the yougstock stage (5 to 10 months) at the start of each time period.

$EBWT_{\text{young [5;10)}}$ = is the empty body weight of youngstock aged five months.

$n_i(t)$ = is the number of individuals present in breeding female stage *i* at the start of each time period.

$$FPI = \frac{\sum_i u_i(t) \cdot EBWT_i - u_{repl.}(t) \cdot EBWT_{repl.}}{\sum_i n_i(t) \cdot EBWT_i^{0.75}}$$

where

FPI = is the flock productivity in terms of net empty body weight (kg) offtake per kg herd metabolic empty body weight and five months time unit at the stationary state.

$u_i(t)$ = is the number of stage *i* animals removed from the herd at the start of each time period.

$EBWT_i$ = is the empty body weight of an animal in stage *i* at the start of each time period.

$n_i(t)$ = is the number of individuals present in stage *i* at the start of each time period.

Tests of significance of differences between energetic efficiency, finite rate of increase (λ) of the herd, reproductive efficiency (*RPI*) and flock productivity (*FPI*) achieved in each of the treatment groups were based on a mixed model ANOVA, with mating season as a fixed and production cycle as a random effect.

Eigenvalue elasticity was used to investigate the proportional contributions of the five different types of matrix entries of the female herd projection matrix (fecundities; survival rates; probabilities of surviving and growing into pregnant stages; probabilities of surviving and growing into nonpregnant stages; and probabilities of remaining in the same stage) to asymptotic herd growth, and thus energetic efficiency once an optimal culling regime has been established. Sensitivity analysis of the non-linear optimization models was used to study the overall impact of changes in conception rate and in age at first breeding on herd productivity. This was motivated by the fact that the latter factors have previously been argued to be major determinants of goat herd productivity under semi-arid conditions in Africa (Peacock, 1983; Wilson, 1989). Both types of sensitivity analyses were performed for the baseline scenario only. They were not carried out for the increased milk offtake scenario because none of the parameters of the corresponding models were derived from field data, but rather were obtained from statistical models which, strictly speaking, can only be considered to provide reliable parameter estimates for the baseline scenario.

7.3 Results

Baseline scenario

Relevant performance measures summarizing results of the herd productivity assessment procedure are presented in Table 7.2. Note that in all model runs the criterion to be maximised was the overall energetic efficiency. Values for the indices of reproductive performance (*RPI*) and flock productivity (*FPI*) were calculated from the solutions to the optimization problems. For the sake of clarity, the solutions themselves, i.e. optimal stage abundances and offtake policies at the steady-state, are not presented for each production cycle×mating season group combination, but only for "average" models which are based on mean parameter estimates by mating season group, pooled over production cycles (Table 7.3). Values for the potential population growth rate (λ), generation time (*A*-), net reproductive rate (R_0), as well as the probability of surviving until the age at first reproduction (*Pmat*) in Table 7.2 were obtained from matrix analyses.

Figure 7.5 illustrates the variability in selected performance measures across production cycles. Parameter estimates obtained for mating season group 1 and 6 in the first and third production cycle, respectively, were such that sustainability at the flock level could not be achieved ($\lambda<1$), and inflows of replacement females of about 17 and 2 percent of their equilibrium stage abundances were necessary to meet the steady-state conditions

Table 7.2. Results of herd productivity assessments by mating season group for the baseline scenario. All values are means over three consecutive production cycles (percentage coefficients of variation in parentheses). Note that values for , *RPI, FPI*, and offtake rates relate to a time unit length of five months. Estimates in a given column without common letters in their superscripts differed at the five percent level of significance.

Mating season	λ	$\bar{A}$ (months)	R_0	$Pmat$	RPI	FPI	Energetic efficiency [%]	Net offtake % of total herd size	Net offtake % of BF* herd size
1	1.036^{ac} (6.7)	39.5^{ad} (2.4)	1.46^{ac} (44.8)	0.490^{a} (33.3)	2.2^{a} (19.4)	0.28^{ac} (48.0)	1.90^{ad} (47.9)	8.7^{a} (54.6)	13.2^{a} (50.6)
2	1.048 (3.9)	43.1^{b} (2.8)	1.60^{ae} (32.3)	0.721^{b} (16.1)	2.9^{b} (8.4)	0.30 (33.8)	1.98^{abd} (38.7)	9.5^{a} (29.1)	15.2^{ab} (30.4)
3	1.085^{ab} (3.0)	42.2^{ab} (1.5)	2.16^{bd} (26.0)	0.756^{c} (13.4)	3.7^{cd} (10.4)	0.40^{b} (16.4)	2.63^{bc} (16.6)	15.0^{b} (13.1)	20.4^{bc} (13.7)
4	1.096^{b} (2.6)	42.5^{ab} (3.5)	2.35^{b} (22.2)	0.663^{d} (19.8)	4.2^{de} (5.1)	0.40^{b} (12.5)	2.78^{c} (12.8)	17.2^{b} (8.9)	21.8^{c} (8.5)
5	1.077^{ab} (2.0)	42.8^{b} (2.1)	1.97^{bde} (16.9)	0.747^{bc} (14.3)	3.5^{c} (10.6)	0.36^{ab} (9.4)	2.44^{abc} (8.7)	16.0^{b} (6.7)	19.7^{bc} (6.9)
6	1.022^{c} (3.5)	48.1^{c} (7.5)	1.26^{c} (33.1)	0.381^{e} (26.8)	2.5^{ab} (11.9)	0.23^{c} (26.6)	1.47^{d} (28.9)	10.2^{a} (53.2)	13.8^{a} (40.8)
Asea-sonal	1.071^{ab} (3.5)	38.5^{d} (0.8)	1.78^{ad} (26.0)	0.625^{f} (17.5)	3.7^{ce} (2.9)	0.37^{ab} (25.8)	2.40^{abc} (23.1)	12.4 (35.5)	18.2 (23.2)

* BF = Breeding female.

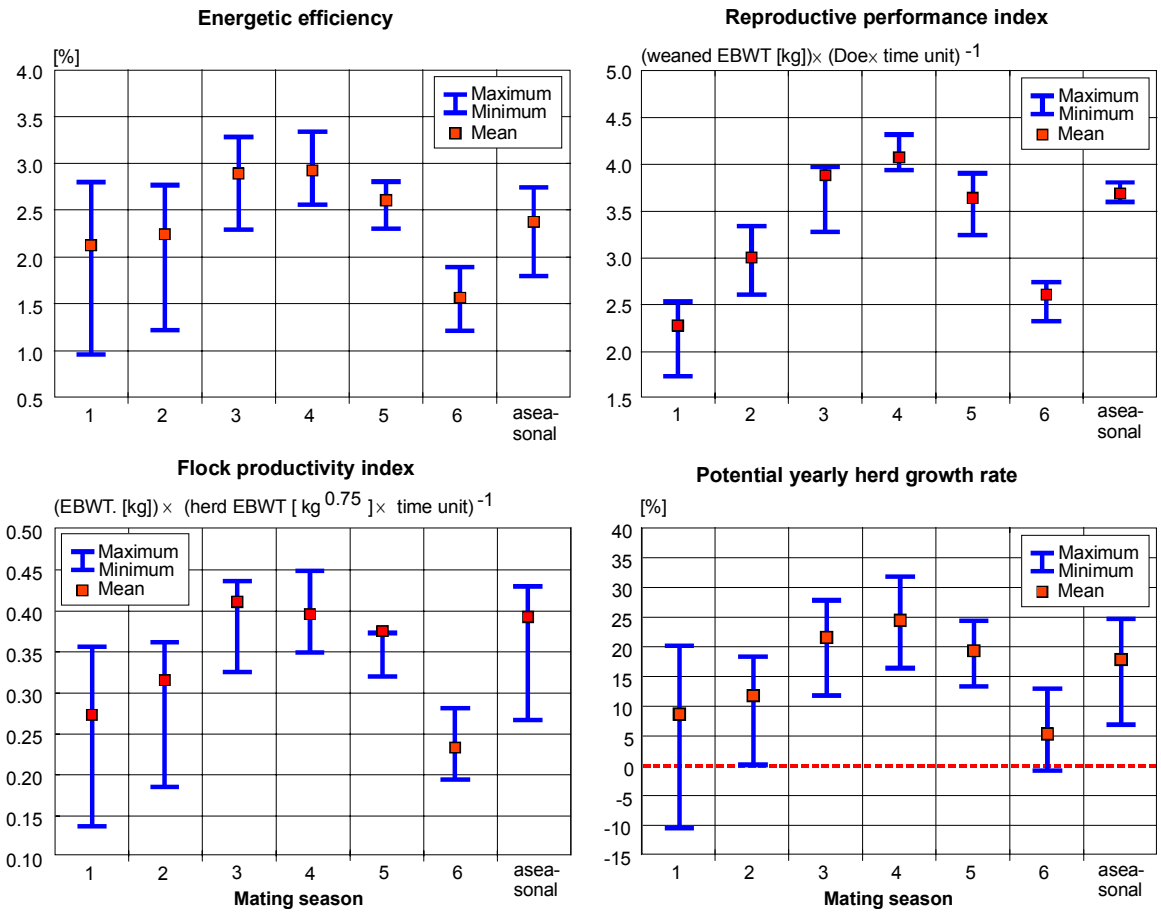

Figure 7.5. Values of selected production efficiency measures by mating season group for the baseline scenario. (EBWT = Empty body weight).

with respect to herd structure and size. Overall, the latter two groups displayed the poorest productivity. The main reason was the small number of female offsprings by which a newborn female individual was expected to be replaced by the end of its life (mean R_0=1.46 and 1.26 for groups 1 and 6). This variable is strongly affected by the probability of survival until maturity (mean *Pmat*< 0.5 in both cases), fecundity and breeding female survival rates.

The entries in Table 7.2 clearly show that mating season group 4 achieved the best performance with respect to all measures, except *Pmat*, which was highest for group 3. At 2.63 percent, energetic efficiency in group 3 was only slightly lower than that for group 4 (2.78 percent), followed in rank order by group 5 (2.44 percent) and the aseasonal reference herd (2.40 percent). Expressed in relative terms, the efficiency of energy conversion in the latter was about 87 percent of that attained in group 4, but this difference was not statistically significant. Markedly lower energetic efficiencies of less than even 2 percent were determined for groups 1 and 2, however the poorest rate of energy conversion of 1.47 percent was achieved in mating season group 6. Pairwise comparisons revealed that energetic efficiency figures for mating season groups 1 and 6 were significantly lower (p< 0.05) than those for groups 3 to 5 and the aseasonal reference herd, whereas for group 2, statistical significance was reached only in comparison to group 4.

Figure 7.5 illustrates the variability in selected performance measures across production cycles. Parameter estimates obtained for mating season group 1 and 6 in the first and third production cycle, respectively, were such that sustainability at the flock level could not be achieved (λ<1), and inflows of replacement females of about 17 and 2 percent of their equilibrium stage abundances were necessary to meet the steady-state conditions with respect to herd structure and size. Overall, the latter two groups displayed the poorest productivity. The main reason was the small number of female offsprings by which a newborn female individual was expected to be replaced by the end of its life (mean R_0=1.46 and 1.26 for groups 1 and 6). This variable is strongly affected by the probability of survival until maturity (mean *Pmat*< 0.5 in both cases), fecundity and breeding female survival rates. The entries in Table 7.2 clearly show that mating season group 4 achieved the best performance with respect to all measures, except *Pmat*, which was highest for group 3. At

2.63 percent, energetic efficiency in group 3 was only slightly lower than that for group 4 (2.78 percent), followed in rank order by group 5 (2.44 percent) and the aseasonal reference herd (2.40 percent). Expressed in relative terms, the efficiency of energy conversion in the latter was about 87 percent of that attained in group 4, but this difference was not statistically significant. Markedly lower energetic efficiencies of less than even 2 percent were determined for groups 1 and 2, however the poorest rate of energy conversion of 1.47 percent was achieved in mating season group 6. Pairwise comparisons revealed that energetic efficiency figures for mating season groups 1 and 6 were significantly lower ($p< 0.05$) than those for groups 3 to 5 and the aseasonal reference herd, whereas for group 2, statistical significance was reached only in comparison to group 4.

Marked differences among mating seasons were also apparent with respect to the variability in energetic efficiency. Coefficients of variation of more than 38 percent were calculated for herds in which mating occurred between February and May (groups 1 and 2), these ranged between only 9 and 17 percent for does joined between June and November (groups 3 to 5). Fairly high levels of variability in herd performance were also observed for group 6 and the aseasonal reference herd (about 29 and 23 percent, respectively).

Reproductive performance (*RPI*) ranged between 2.2 (group 1) and 4.2 kg (group 4) of weaned empty body weight per doe over a five months period. Likewise to energetic efficiencies, the highest reproductive performances were achieved in mating seasons 3 to 5 and in the aseasonal reference herd. The lowest values were again calculated for groups 1, 2, and 6. A similar distribution pattern was characteristic of the flock productivity index (*FPI*), that ranged between 0.23 (group 6) and 0.4 kg (group 4) of empty body weight offtake per kg herd metabolic empty body weight.

Besides yield levels in terms of milk production and body weight development, the most important factor that determined energetic efficiency at the herd level was the potential or asymptotic rate of population growth, λ. This parameter subsumes the joint effects of vital rates, i.e. reproduction, survival, and development, on population dynamics, and therefore offtake rates. As may be seen from Table 7.2, mean energetic efficiencies and asymptotic growth rates followed almost the same patterns, and indeed correlation analysis revealed a strong linear relationship between both entities (r=0.98, $p< 0.001$). A logical consequence of this is that energetic efficiency must also be closely related to the net reproductive rate (r=0.96, $p< 0.001$), since the latter is, by definition, one of the two factors determining λ ($\ln \lambda = \ln R_{\square\square} / T$, T=time required for a population at stable stage distribution to grow by the net reproductive rate). When converted to annual percentage growth rates ($100\times[\lambda^{2.4}-1]$), joining goats in season 4 would result in an annual increase of goat flocks of almost 25 percent, compared to only about 5 percent in season 6 ($p< 0.005$). These, of course, are theoretical values which would only be achieved if vital rates remained constant over time, but they nevertheless indicate that the choice of the breeding season may have a large impact on herd growth and therefore offtake rates and production efficiency. The annualised potential rate of increase for the aseasonal reference flock (approximately 18 percent) was about 73 percent of that achieved in mating season group 4, but this difference was not statistically significant.

Consistent with expectation, generation time was markedly shorter in the aseasonal reference flock (38.5 months) than in seasonal breeding groups except for group 1 ($p< 0.05$), due to the shorter period between successive mating events than that implied by a seasonal breeding regime. The mean generation time of 39.5 months for group 1, however, also emphasizes the effect of conception rates, which was the highest in this group, on *A*-. This is best seen when comparing mean generation time in the latter group with that of mating season 2 (43.1 months), in which the average probability of conception was particularly low (82.7 percent). Given that the difference in doe survival over lactation and pregnancy stages between both groups was small, leading to similar stable stage abundances in breeding female stages, the lower probability of conception implied that, in mating season 2, a larger proportion of replacement and breeding females would be expected to spend one or more production cycles in an unreproductive stage, thus increasing the average age at all kiddings. With a mean generation length of 48.1 months, this effect was even more pronounced in group 6. Estimated probability of conception was also low in this group (86.1 percent), and its impact on generation time was compounded by the fact that higher stable stage abundances of older does were predicted than in the first two mating seasons, because of lower mortality rates over lactation and pregnancy stages for higher parity does.

Table 7.3. Optimal steady state stage distributions and culling policies (percentage stage abundances and offtake rates) in each mating season group for the baseline scenario, obtained from runs of "average" models.

Stage	time interval in months	Mating season													
		1		2		3		4		5		6		aseasonal	
		abund-ance	off-take	abund-ance	off-take	abund-ance	off-take	abund-ance	off-take	abund-ance	off-take	abund-ance	off-take	abund-ance	off-take
Fem. young	[0, 5)	11.4	0	8.0	0	10.2	0	11.1	0	10.0	0	12.9	0	11.5	0
	[5, 10)	6.0	0	6.3	0	8.4	0	9.8	0	9.1	0	8.1	0	8.5	0
Male young	[0, 5)	11.4	0	8.0	0	10.2	0	11.1	0	10.0	0	12.9	0	11.5	0
	[5, 10)	6.0	0	6.3	0	8.4	0	9.8	100	9.1	100	8.1	100	8.5	0
Male surplus	[10, 15)	6.0	0	6.1	0	8.4	100							7.9	100
	[15, 20)	5.7	0	5.9	0										
	[20, 25)	5.6	100	5.9	0										
	[25, 30)			5.9	100										
BF replacement		6.0	0	6.1	0	8.4	0	8.6	0	8.4	0	5.5	0	7.9	0
BF preg. parity 0		5.6	0	5.7	0	6.7	0	6.7	0	7.1	0	4.9	0	7.2	0
BF open parity 0,	[0, 5)	0.2	0	1.0	0	1.1	100	0.8	100	0.5	100	0.7	0	0.8	0
	[5, 12)	0.3	0	1.4	0							0.9	0	0.1	0
	[12, 17)	0.0	0	0.2	100							0.1	0	0.0	100
	[17, 24)	0.0	0									0.1	0		
	[24, 29)	0.0	100									0.0	100		
BF lactating parity 1		7.8	0	7.9	0	9.3	0	9.3	0	9.9	0	6.8	0	7.0	0
BF preg. parity 1		5.1	0	4.5	0	5.7	0	5.9	0	6.6	0	4.7	0	6.5	0
BF open parity 1,	[0, 5)	0.2	100	0.9	100	0.9	100	0.7	100	0.5	100	0.7	0	0.8	56.3
	[5, 12)											0.9	0	0.0	100
	[12, 17)											0.1	100		
BF lactating parity 2		7.0	0	6.1	0	7.6	0	8.2	0	9.1	0	6.5	0	6.1	0
BF preg. parity 2		4.2	0	3.4	0	4.6	9.8	5.2	3	6.0	8.3	4.0	0	5.3	0
BF open parity 2,	[0, 5)	0.2	100	0.7	100	0.8	100	0.7	100	0.5	100	0.6	100	0.7	100
BF lactating parity 3		5.7	0	4.4	0	5.5	0	7.0	0	7.7	0	5.4	0	5.0	0
BF preg. parity 3		3.2	81.5	2.4	71.9	3.3	100	4.4	100	5.1	100	3.3	10.1	4.3	100
BF open parity 3,	[0, 5)	0.1	100	0.5	100	0.5	100	0.6	100	0.4	100	0.5	100	0.5	100
BF lactating parity 4		0.8	0	0.9	0	0.0	0	0.0	0	0.0	0	4.0	0	0.0	0
BF preg. parity 4		0.4	0	0.5	0	0.0		0.0		0.0		2.4	0	0.0	
BF open parity 4,	[0, 5)	0.0	100	0.1	100	0.0		0.0		0.0		0.4	100	0.0	
BF lactating parity 5		0.5	0	0.5	0	0.0	0	0.0	0	0.0	0	2.8	0	0.0	0
BF cull for age		0.4	100	0.5	100	0.0		0.0		0.0		2.8	100	0.0	

Average offtake rates per 5 months time unit in relation to total herd size at the stationary state ranged between 8.7 percent in mating season 1 and 17.2 percent in mating season 4. Offtake rates in groups 3 to 5 were found to be significantly higher than in groups 1, 2, and 6. Variability in offtake rates was again markedly higher in the latter groups and in the aseasonal reference herd. In order to accommodate variations in the size of the male herd, in Table 7.2 offtake rates are also given in relation to the steady-state abundance of breeding females. For instance, because of the larger proportion of males maintained in the first two mating seasons (Table 7.3), their performance relative to the other mating season groups was slightly improved when compared on the basis of offtake per breeding female in the herd. Nevertheless, ranking of mating season groups with respect to both offtake rate measures was almost identical to that described previously for herd performances in terms of energetic efficiency.

An important result emerging from the herd productivity assessment procedure was that in all mating seasons, optimal offtake per animal in the herd per time unit exceeded the respective asymptotic population growth rate (λ), as derived through matrix analyses. To clarify this issue, values of λ (expressed in percent increase per 5 months period), offtake rate by mating season group, and as well as of the maximum *proportional* offtake rates that would keep the herd level constant from one period to the next are plotted in Figure 7.6. (In case of a herd subjected to a pre-reproductive harvesting schedule, maximum proportional offtake rate can be calculated as $[100\times(\lambda-1)]/\lambda$, if population growth rate is greater than or equal to 1). Potential population growth rates were between 38 (mating season 3) to as much as 84 percent (mating season 6) lower than optimal offtake rates determined by the herd productivity assessment procedure. Similarly, an offtake policy which harvests an equal proportion of individuals from each stage class would result in offtake rate levels of only 16 (mating season 6) to 56 percent (mating season 3) of those determined by non-linear programming. Hence, by comparison with the situation without active management controls (as described by average R_0 and λ values obtained through matrix analyses), optimising herd structure and culling policy with respect to energetic efficiency resulted in stationary state stage abundances which maximized net reproductive rates, and therefore offtake per time unit.

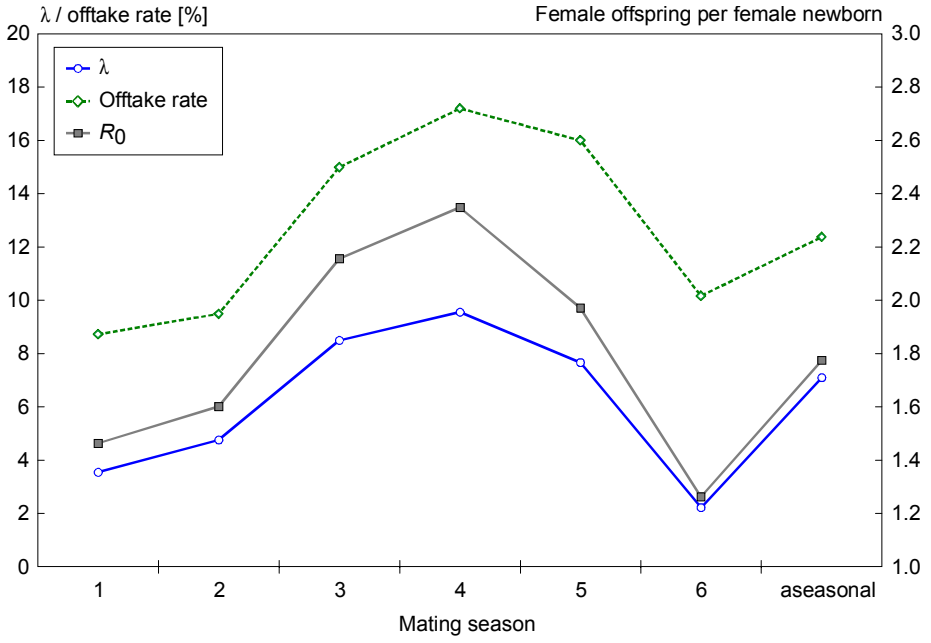

Figure 7.6. Values of λ (in percent increase per 5 months time unit), optimum offtake rate, and maximum proportional offtake rate according to mating season group for the baseline scenario ("average" models).

In general, keeping breeding females in the herd beyond the third parturition was found to be adequate only in situations where asymptotic population growth rate was lower than 5 percent per five months period (groups 1, 2 and 6). In all other cases, breeding females were culled after completing their third lactation, i.e. upon entering parity 3 pregnancy or open stages (Table 7.3). Also, non-pregnant breeding females were only kept in herds with insufficient growth potential (groups 1, 2 and 6), but this was limited to does with at most one prior lactation. Culling policies for non-pregnant does in the aseasonal herd differed from this general pattern because of the shorter time period between successive mating events. Here, the optimal culling strategy consisted of keeping reproductively inactive breeding females at least for another 10 months or two matings

(nulliparous does) or for at most 5 months or one mating event (primiparous does) in the herd, while in higher parity stages does were immediately culled when they failed to conceive.

An additional result to note is that in none of the herds modelled female youngstock were reared as surplus females (Table 7.3). In all cases considered it was more efficient to rear them as replacements and to exploit their potential to contribute to future herd growth and to the production of male surplus animals. The optimal culling age for the latter ranged between 5 and 25 months, and there was a tendency for an increase in optimal culling age with decreasing potential population growth rate and, hence, energetic efficiency (groups 1, 2, and 3). Optimal decisions rules for mating season 6 differed from this trend due to the excessive mortality in youngstock after weaning. However, it should be emphasized that decisions relating to the management of surplus male stages are not independent of the performance, in terms of energetic efficiency, achieved by the female part of a herd. This leads to very complex decision rules which are difficult to predict beforehand.

Based on "average" herd growth models for mating seasons 1 and 4, Figure 7.7 illustrates how optimal culling ages for male surplus animals may differ depending on the level of energetic efficiency achieved in the remaining herd. The plot on the left shows that considering gross energy outputs produced and total metabolizable energy consumed in the surplus males herd only, energetic efficiency was a strictly declining function of culling age. This is to be expected, since cumulative metabolizable energy requirements grow at a much faster rate than gross energy accumulation in the body with increasing age. From this perspective, fattening of male animals beyond five months of age is certainly not optimal when the conversion efficiency of metabolizable feed energy to gross energy content in edible products is to be maximized. However, when metabolizable energy costs required and gross energy outputs produced by the female part of the herd, which is supplying male young for fattening, were taken into account, the picture changed dramatically.

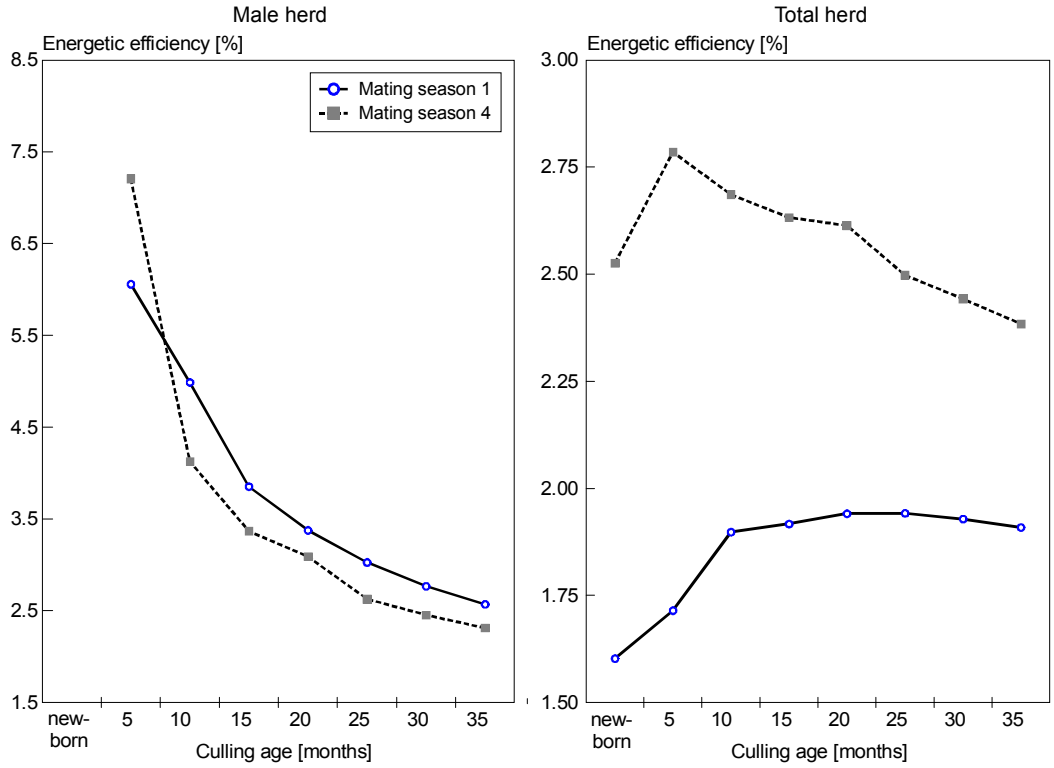

Figure 7.7. Effects of culling age of male surplus animals on energetic efficiency determined at the male herd and total herd level for mating season groups 1 and 4 ("average" models). Note that energetic efficiencies for the newborn stage could not be calculated by considering the male herd only since, at birth, cumulative metabolizable energy requirements were assumed to be equal to zero.

The plot on the right in Figure 7.7 shows that for a herd in which the process of producing male animals for fattening is rather inefficient, such as in mating season 1, the optimal culling age should be extended well beyond 15 months of age. In contrast, the optimal culling time point is reached much earlier at around 5 months of age in mating season group 4, which is the most efficient one with respect to reproductive performance.

Sensitivity analysis of the results of the baseline scenario

Elasticities of λ with respect to changes in fecundities, survival rates, and probabilities of surviving and growing into pregnant stages for "average" projection matrix pertaining to the six mating season groups and the aseasonal reference herd are shown in Tables 7.4 and 7.5. Note that because elasticities sum to one, for each mating season treatment the relative contribution of the matrix elements to λ can be compared. The three groups of parameters shown in the above figures together account for 86 (mating season 6) to 93 percent (aseasonal herd) of the contributions of all matrix entries to population growth. The other two groups, i.e., probabilities of surviving and remaining in the same stage and probabilities of surviving and moving into nonpregnant stages (elasticities of λ to these entries are not shown graphically), are thus relatively unimportant parameters in terms of their impact on λ. The largest changes in asymptotic herd growth can be expected to occur when survival rates of female youngstock and fertile female replacements are perturbed (Tables 7.4 and 7.5), either due to environmental factors, or as a consequence of management interventions. About one third of all contributions to l come from these three matrix coefficients. An increase in fecundity rates, in contrast, can be seen to have a rather limited impact on herd growth and productivity (Table 7.4).

Table 7.4. Elasticities of herd growth rate to fecundity and survival rates for the six mating season groups and the aseasonal reference herd (BF = breeding female). Calculations were based on "average" projection matrices (baseline scenario).

		Mating season						
Stage	time interval in months	1	2	3	4	5	6	asea-sonal
BF replacement		0.121	0.099	0.106	0.106	0.112	0.090	0.117
BF open parity 0,	[5, 12)	0.004	0.014	0.012	0.010	0.006	0.012	0.001
	[17, 24)	< 0.001	0.002	0.001	0.001	< 0.001	0.001	< 0.001
	[29, 36)	< 0.001	< 0.001	0.000	0.000	< 0.001	< 0.001	-
BF lactating parity 1		0.090	0.073	0.076	0.079	0.084	0.073	0.087
BF open parity 1,	[5, 12)	0.003	0.010	0.008	0.007	0.005	0.009	0.001
	[17, 24)	< 0.001	0.001	0.001	0.001	< 0.001	0.001	< 0.001
BF lactating parity 2		0.060	0.049	0.050	0.055	0.059	0.055	0.061
BF open parity 2,	[5, 12)	0.002	0.006	0.005	0.005	0.003	0.007	0.001
	[17, 24)	< 0.001	0.001	0.001	< 0.001	< 0.001	0.001	< 0.001
BF lactating parity 3		0.034	0.027	0.029	0.033	0.036	0.035	0.036
BF open parity 3,	[5, 12)	0.001	0.003	0.003	0.003	0.002	0.004	< 0.001
	[17, 24)	< 0.001	< 0.001	0.000	< 0.001	< 0.001	< 0.001	< 0.001
BF lactating parity 4		0.013	0.010	0.011	0.013	0.015	0.016	0.015
BF open parity 4,	[5, 12)	< 0.001	0.001	0.001	0.001	0.001	0.002	< 0.001
	[17, 24)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

In order to enhance goat herd productivity in the current production system, management interventions should therefore not primarily be directed towards increasing reproductive output of breeding females. Another consequence of the low elasticities of λ to perturbations in fecundity rates is that model predictions generated in this study can tolerate somewhat larger uncertainties in these parameters than in juvenile and subadult survival. These findings are contrary to the results of a sensitivity analysis reported by Peacock (1984), which was aimed at identifying major factors affecting levels of biological productivity in Maasai goat herds. According to this study, the number of kids born per year was a major determinant of biological productivity. The impact of changes in the probabilities of surviving and moving into pregnancy stages are somewhat more difficult to interpret, since these entries depend on both the probability of conception and that of surviving over the corresponding stage. However, it can be seen from Table 7.5 that the probability with which female replacements survive and conceive plays an important role in determining overall herd growth rate. The impact of this type of matrix entry declines over successive parturitions due to the reduction in residual reproductive value with advancing parity stage.

Table 7.5. Elasticities of herd growth rate to probabilities of surviving and moving into pregnant stages for the six mating season groups and the aseasonal reference herd (BF = breeding female). Calculations were based on "average" projection matrices (baseline scenario).

		Mating season						
Stage	time interval in months	1	2	3	4	5	6	asea-sonal
BF replacement		0.121	0.099	0.106	0.106	0.112	0.090	0.117
BF open parity 0,	[5, 12)	0.004	0.014	0.012	0.010	0.006	0.012	0.001
	[17, 24)	< 0.001	0.002	0.001	0.001	< 0.001	0.001	< 0.001
	[29, 36)	< 0.001	< 0.001	0.000	0.000	< 0.001	< 0.001	-
BF lactating parity 1		0.090	0.073	0.076	0.079	0.084	0.073	0.087
BF open parity 1,	[5, 12)	0.003	0.010	0.008	0.007	0.005	0.009	0.001
	[17, 24)	< 0.001	0.001	0.001	0.001	< 0.001	0.001	< 0.001
BF lactating parity 2		0.060	0.049	0.050	0.055	0.059	0.055	0.061
BF open parity 2,	[5, 12)	0.002	0.006	0.005	0.005	0.003	0.007	0.001
	[17, 24)	< 0.001	0.001	0.001	< 0.001	< 0.001	0.001	< 0.001
BF lactating parity 3		0.034	0.027	0.029	0.033	0.036	0.035	0.036
BF open parity 3,	[5, 12)	0.001	0.003	0.003	0.003	0.002	0.004	< 0.001
	[17, 24)	< 0.001	< 0.001	0.000	< 0.001	< 0.001	< 0.001	< 0.001
BF lactating parity 4		0.013	0.010	0.011	0.013	0.015	0.016	0.015
BF open parity 4,	[5, 12)	< 0.001	0.001	0.001	0.001	0.001	0.002	< 0.001
	[17, 24)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

Given that probabilities of surviving and moving into pregnant stages are derived parameters, it is worthwhile investigating the impact of the underlying vital rates on population growth. In the present context, it was of particular interest to elucidate the potential effect of perturbations in conception rates on potential herd growth and productive efficiency. This is because conception rates can be difficult to assess in the field, and it is therefore important to obtain some information on how errors in the parameter estimation may affect model predictions. Results of the sensitivity analysis of conception rates are presented here for the baseline scenarios of mating season groups 1 and 4 only, being representative of goat herds with low and high potential growth rates and productive efficiencies. The corresponding non-linear optimization models were rerun with the original conception rates altered, respectively, by –30 to +3.5 percent, and by –30 to +12.5 percent (Figure 7.8). In absolute terms, this amounted to testing the impact of a change in conception rates over the range from 67 to 100 percent for mating season group 1, and from 62 to 100 percent for mating season group 4. Note that, in contrast to eigenvalue-elasticities, the so-obtained proportional changes in population growth and productive efficiency plotted in Figure 7.8 do not sum to 1 over all underlying variables, nor do they represent the contributions of the individual variables to λ in the sense used before (see Caswell (1989:136) for further explanations).

Overall, responses in terms of productivity tend to be less-than-proportionate to the perturbations in conception rates, while population growth rates appears to react more than proportionately to variations in this variable. The response curves in Figure 7.8 also reveal that the effects of changes in conception rates on herd dynamics and productivity depend on the initial herd growth rate. Response are more pronounced in initially slowly growing herds than in fast growing herds. Thus, management interventions that rely upon manipulating conception rates in order to improve herd productivity will be less effective at high than at low levels of herd growth. For the presently chosen life-cycle structure of goat herds, estimation accuracy of conception rates appear to be more important in determining asymptotic herd growth than productive efficiency. As indicated by sensitivity analysis, predicted productivity levels will be affected by less than ±10 percent as long as errors in estimation of conception rates range between ±15 to ±20 percent.

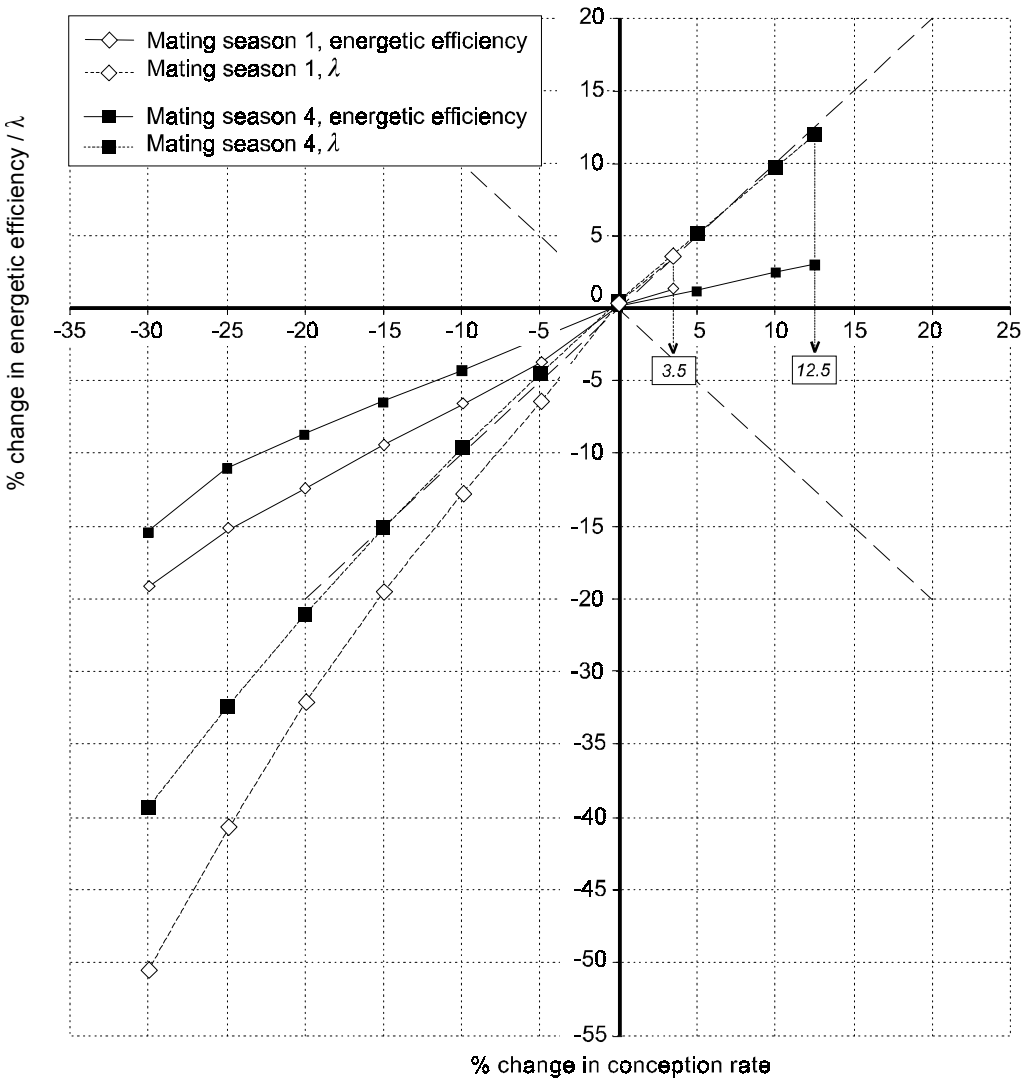

Figure 7.8. Effect on asymptotic herd growth rate of proportional changes in conception rate by +3.5 to –30 percent (group 1, corresponding to conception rates of 100 to 67 percent) and +12.5 to –30 percent (group 4, corresponding to conception rates of 100 to 62 percent). Calculations for mating season groups 1 and 4, based on "average" projection matrices (baseline scenario).

Sensitivity analysis with respect to age at first breeding was based on the same approach as that used for conception rates, and involved changing the original parameter values by –33.3 to +33.3 percent or, in absolute terms, from 10 to 20 months at one monthly steps. Results of this part of the analysis are again presented graphically for mating season groups 1 and 4 in Figure 7.9. Generally, changes in age at first breeding tend to have a larger impact upon herd growth rate than upon herd productivity. Reducing age at first breeding from 15 to 10 month (a 33.3 percent decrease) increased energetic efficiencies by only 12.1 (mating season 1) and 17.8 percent (mating season 4), while the same parameter changes had an almost proportionate impact upon herd growth. Similarly to conception rates, the effect of a given proportionate change in age at first breeding on herd productivity is clearly dependent on the initial magnitude of herd growth rate. If λ is large (mating season 4), decreasing developmental time will have a larger effect on overall productivity than at low levels of λ (mating season 1).

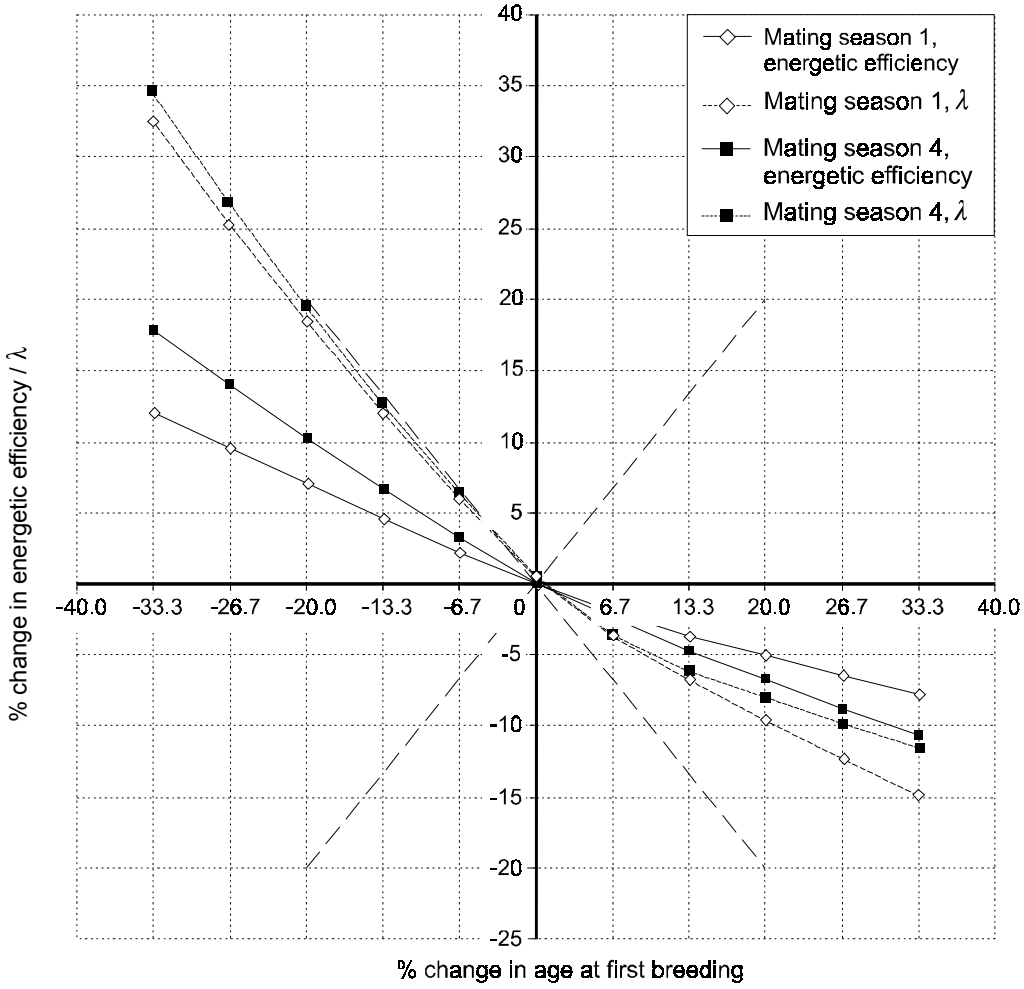

Figure 7.9. Effect on asymptotic herd growth rate of proportional changes in age at first breeding over the range from 10 (a decrease of 33.3 percent from an initial value 15 months) to 20 months (an increase of 33.3 percent from an initial value 15 months). Calculations for mating season groups 1 and 4, based on "average" projection matrices (baseline scenario).

It should be stressed that the above results were obtained by making the assumption that changes in age at first breeding neither affect vital rates, especially conception, fecundity, and survival of breeding females, during the first, nor over subsequent reproductive cycles. If, however, strong interactions among life history traits exist, even large changes in age at first breeding might fail to produce the responses in asymptotic growth and herd productivity as depicted in Figure 7.9. A reduction in age at first breeding, in particular, is likely to embody a trade-off between current reproduction and future survival and /or fecundity patterns, a fact which has not been taken into account in conducting the sensitivity analysis. Data from the current experiment indicated that poor body weight development of does may be detrimental to their survival and productive performance, the most important of which is milk production. Insufficient milk availability until weaning, in turn, has been shown to expose kids to a very large risk of death. As youngstock survival is of paramount importance to herd dynamics and productivity, reducing the age at first breeding may prove to be a far less attractive management strategy than has previously been suggested, for instance, by Wilson (1989). More specifically, changes in developmental time will tend to have the smallest effect on herd growth rate and productivity in slowly-growing or stationary herds in which juvenile mortality is already high.

Increased milk offtake scenario

Means values of performance measures by mating season group for the increased milk offtake scenario are given in Table 7.6. The increased milk offtake for human consumption implied an increase in juvenile mortality, as reflected by the uniform decrease in probabilities of surviving until maturity compared to those reported for the baseline scenario. Consequently, potential population growth rates and net reproductive rates were also lower than in the baseline scenario.

Table 7.3. Optimal steady state stage distributions and culling policies (percentage stage abundances and offtake rates) in each mating season group for the baseline scenario, obtained from runs of „average“ models.

Mating season	λ	$\bar{A}$ (months)	R_0	$Pmat$	RPI	FPI	Energetic efficiency [%]	Net offtake % of total herd size	Net offtake % of BF* herd size
1	1.013	41.0^{ac}	1.24^{a}	0.411^{a}	1.7^{a}	0.25^{ac}	2.39	7.8^{a}	11.2^{a}
	(7.3)	(2.4)	(48.0)	(38.0)	(25.1)	(52.8)	(50.5)	(64.3)	(60.3)
2	1.029	44.5^{a}	1.41^{a}	0.624^{bc}	2.2^{ab}	0.27	2.50	10.1^{ab}	13.7^{ab}
	(5.3)	(1.0)	(41.1)	(26.5)	(23.0)	(42.4)	(39.6)	(51.9)	(45.9)
3	1.080^{a}	42.6^{ac}	2.04^{b}	0.722^{b}	3.3^{c}	0.36^{ab}	3.49^{a}	15.7^{b}	19.5^{b}
	(2.0)	(2.0)	(18.5)	(6.7)	(6.2)	(14.6)	(6.6)	(9.1)	(9.3)
4	1.086^{a}	43.2^{ac}	2.16^{b}	0.610^{c}	3.7^{c}	0.38^{b}	3.60^{a}	16.5^{b}	21.0^{b}
	(2.0)	(3.1)	(18.1)	(15.0)	(3.3)	(13.1)	(11.6)	(7.7)	(7.7)
5	1.064^{a}	43.6^{ac}	1.78^{ab}	0.676^{bc}	3.2^{b}	0.33^{ab}	3.30^{a}	15.3^{b}	18.8^{b}
	(1.7)	(1.7)	(15.0)	(16.0)	(10.0)	(8.5)	(10.5)	(4.6)	(4.5)
6	0.966^{b}	53.5^{b}	0.78^{c}	0.234^{d}	1.5^{a}	0.18^{c}	2.00^{b}	8.3^{a}	10.8^{a}
	(7.6)	(14.7)	(73.4)	(68.5)	(74.6)	(36.5)	(27.7)	(76.1)	(73.4)
Asea-sonal	1.059^{a}	39.0^{c}	1.63^{ab}	0.573^{c}	3.2^{b}	0.33^{ab}	3.08^{a}	13.9	18.0
	(3.8)	(1.5)	(28.5)	(21.1)	(11.5)	(26.4)	(25.2)	(27.0)	(23.0)

* BF = Breeding female.

Mating season groups 1, 2 and 6 were most affected by the simulated change to a dual meat and milk production system, with mean values of λ being reduced by 65, 40, and as much as by 251 percent, respectively. The average decrease in λ was lowest in group 3 with only 6 percent, followed in rank order by group 4 (10 percent), 5 (16 percent), and the aseasonal reference flock (18 percent). Significant differences in λ were only detected between the latter groups and mating season 6 ($p< 0.05$) which, on average, was not sustainable (λ=0.966) and an inflow of replacement females of about 13 percent of their equilibrium stage abundances was required to achieve constancy of herd size and structure. Upon shifting stable stage abundances towards higher parity does, the increase in juvenile mortality also led to a general increase in generation time, which, again, was most pronounced in group 6 (48.1 vs. 53.5 months).

By comparison with the baseline scenario, average herd productivity in terms of energetic efficiency improved between 26 percent in group 1 and 36 percent in group 6 (Figure 7.10), while the relative ranking of mating season groups with respect to this criterion remained unaffected by the simulated change in production strategy. Significant differences in energetic efficiency occurred only between mating season group 6 and groups 3, 4, 5 and the aseasonal reference flock ($p< 0.05$).

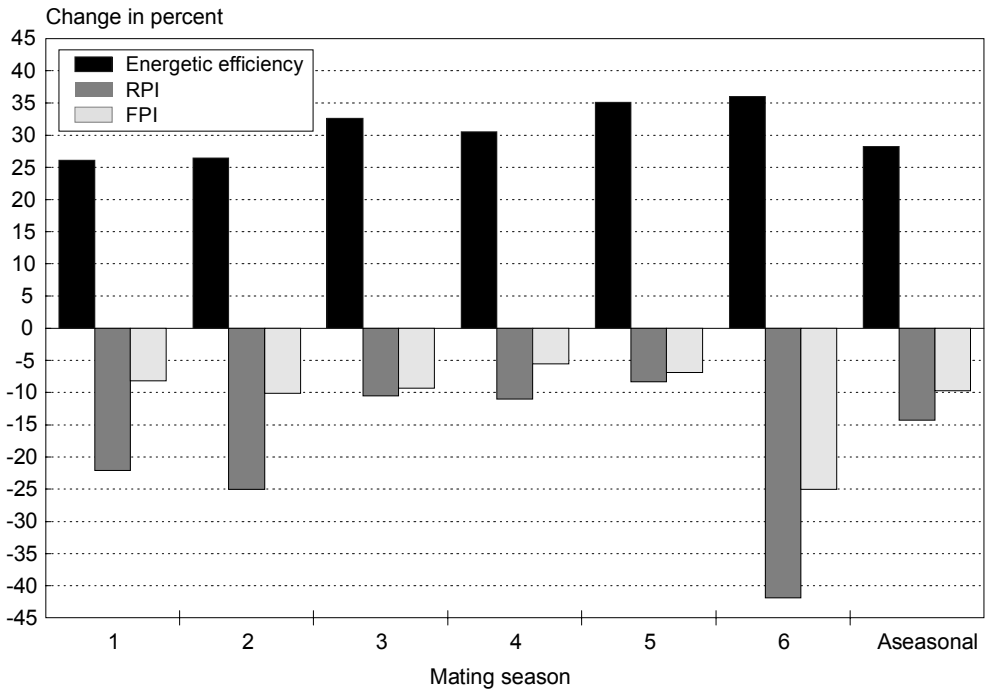

Figure 7.10. Changes in energetic efficiency, *RPI*, and *FPI* in the increased milk offtake scenario relative to the baseline scenario.

As one might expect, reproductive performance (*RPI*) and flock productivity (*FPI*) were negatively affected by higher juvenile mortality rates and reduced growth rates in kids. *RPI* and *FPI* values were 10 (group 5) to 42 percent (group 6) and 6 (group 4) to 25 percent (group 6) lower than in the baseline scenario, respectively (Figure 7.10). However, for both indices the resultant ranking of mating season groups was not affected, except that the lowest *RPI* value was observed in group 6 instead of group 1, as in the baseline scenario.

There was no clear cut pattern of change in offtake levels in relation to total herd size, and the differences between both scenarios were generally small. In contrast, offtake levels in relation to the breeding female herd size were consistently lower in the increased milk offtake scenario. On the one hand, this was due to the fact that fewer male animals survived to culling age. On the other hand, higher juvenile mortality rates also reduced the number of female youngstock available as replacements and, concomitantly, led to increases in breeding female herd sizes. Generally, there was a tendency to replace breeding females, at least partly, in later parity stages than in the baseline scenario. This was mainly due to the necessity to compensate for the reduced potential population growth rates.

7.4 Discussion

Comparison of estimated levels of energetic efficiency

This section discusses the range of energetic efficiencies obtained in this work to those published in the literature for other grazing systems. Analyses of energy flows and efficiencies of energy transformation from one trophic level to another were first introduced by ecologists to describe ecosystem organization and functioning (Odum, 1969), but more recently have also been used to investigate energetic pathways and conversion efficiencies in and among pastoral grazing ecosystems (Coughenour et al., 1985; Ellis et al., 1979; Western, 1982), and as a means for comparing levels of biological efficiency achieved in different livestock production systems (de Ridder and Wagenaar, 1986). Some of the energetic efficiency figures obtained in the latter studies can be used as benchmarks against which the results of this work can be compared (Table 7.7). All figures were originally given in terms of gross energy output for human consumption in relation to gross energy intake of livestock. Since in the present study forage input was defined in terms of metabolizable energy intake, the published ratios were converted to this scale by dividing them by a conversion factor of 0.405, obtained upon assuming an average digestibility of 0.5 and a ratio of metabolizable energy to digested energy of 0.81 (Konandreas and Anderson, 1982).

Table 7.7. Percentage energetic efficiency of some grazing systems, defined as the ratio of gross energy output for human consumption divided by metabolizable forage energy intake.

Source	Grazing system	Livestock Species	Energetic efficiency [%]
Coughenour et al., 1985	Turkana, pastoral	Sheep and goat	1.93
		Cattle	2.15
		Camel	2.96
	U.S. Western, ranching	Cattle	13.60
de Ridder and Wagenaar, 1986	Botswana, traditional	Cattle	3.09
	Botswana, ranching	Cattle	6.35
Ellis et al., 1979	Karimojong, pastoral	Cattle	1.48

From Table 7.7, it can be seen that the energetic efficiencies computed for both the baseline and increased milk offtake scenarios are within the range of values reported for other pastoral production systems. The dual purpose meat and milk production scenario uniformly increased efficiencies by 26 to 36 percent compared to the baseline scenario. Nevertheless, the herd of SEA goats studied in this experiment seemed to demonstrate relatively low forage energy conversion efficiencies when compared to commercial cattle ranching systems. Production efficiency is probably constrained by environmental factors such as poor forage quality, water and heat constraints on intake, and sparse and unequal distribution of forage and water resources which cause high energy investments in self-maintenance (Coughenour et al., 1985; Western, 1982). The solutions to the herd productivity assessment models considered in the present work revealed that milk composed between 2 and 4.5 percent of total gross energy output for human consumption in the baseline scenario, and between 9.9 and 15.3 percent in the increased milk offtake scenario. By contrast, for the Turkana pastoral production system Coughenour et al. (1985) estimated that 70.1 percent of pastoral food energy extracted from sheep and goat herds were obtained in form of milk. On the one hand, the large discrepancy between these estimates may be due to the fact that Turkana pastoralists achieve much higher milk offtake rates from their sheep and goat herds than the one third of total lactational milk yield assumed in the increased milk offtake scenario. On the other hand, when considering the comparatively low rate of ecological efficiency achieved in Turkana smallstock herds (Table 7.7), it may also indicate that the production objective of Turkana herders differs from that assumed in assessing herd productivity in this work. Maximizing energetic efficiency subject to keeping total herd size constant invariably implies that animals are disposed of at the optimum biological moment. By contrast, from the perspective of pastoral producers a substantial part of the benefits of livestock keeping may be derived from the maintenance and accumulation of large animal biomasses. Ultimately, one of the main incentives for pursuing these goals is likely to be the need to reduce the risk of losing the entire herd. This aspect of pastoral herd management obviously has not been accommodated for in the herd productivity assessment procedure.

Optimum mating season

The results of the herd productivity assessment lead to the conclusion that under the prevailing environmental conditions, confining breeding in pastoral goat herds to the period from June to July (mating season 4) confers a distinctive advantage in terms of all relevant biological efficiency parameters considered. From a practical standpoint, however, there is probably little basis on which to differentiate between mating seasons 3 and 4, the latter performing only slightly better than the former in terms of all performance criteria calculated. The present results, therefore, concur with Wilson (1984) and Wilson et al. (1985) who found that dams which gave birth in the hot dry season in mono-modal rainfall regimes in Mali and Sudan and in the analogous short dry season in southern Kenya showed the best performance as measured by a productivity index defined as average total litter liveweight at 150 days produced per doe and year (the so-called ILCA Index I, named after the former International Livestock Center for Africa). Thus, there appears to be some justification for the management practice of Maasai pastoralists in southern Kenya to try to limit breeding activity in their goat flocks to the beginning of the dry season in June, so that births occur during the short dry season (de Leeuw et al., 1991).

Contrary to expectations, the relative ranking of mating season groups was not affected by the simulated increase in milk offtake for human consumption. Such a change in management strategy reduces *reproductive* performance (as measured, for instance, by the RPI criterion) through a negative impact on kid survival, which increases at an accelerating rate with declining milk availability for suckling kids. On the other hand, these losses tend to be offset by the rise in energy output from the system due to the higher milk offtake rates for human consumption. Based on these considerations, a change in relative ranking of mating season groups with respect to overall energetic efficiency could have been expected to arise among group 4 on the one hand, and groups 3 and 5 on the other, given that mean total lactational milk yields in the latter two groups exceeded that in group 4. However, this difference in milk yields, as well as the relatively larger increase in kid mortality in mating season 4 associated with the reduced availability of milk for youngstock were not sufficient to compensate for the initial gap in productive efficiency between groups 3 and 5 on the one hand, and group 4 on the other.

The results of the increased milk offtake scenario clearly show that productivity measures such as RPI and FPI cannot be used to assess technical efficiency of livestock production systems when a significant proportion of total benefits are derived in terms of products other than live animals for sale, slaughter, or herd accumulation. This was illustrated by the effect of a reduction of milk availability for suckling kids, which, through higher mortality and slower growth, lead to a uniform decrease in both the RPI and FPI indices, while, by contrast, the simultaneous rise in energetic efficiency adequately reflected the positive effect of such a shift to a dual-purpose production system on biological herd productivity. By the same token, this study confirms the contention frequently advanced by ecologists that, while milk consumption diverts energy from youngstock and reduces their survival and growth rates, energy transfer to humans through milk, or through a combination of milk and meat is still (energetically) more efficient than transfer through meat alone (Coughenour et al., 1985; Western, 1982; Western and Finch, 1986).

If maximum energetic efficiency is to be achieved, breeding of goats in the period from December to May should be avoided, irrespective of the amount of milk extracted for human consumption. The poor performance of mating season groups 1, 2 and 6 was mainly due to elevated kid and doe mortality rates. In all three groups, significant parts of the lactation stage coincided with the long dry season, during which feed availability was insufficient to cover the nutrient requirements of dams and their progeny. This effect was particularly pronounced in mating season group 1, in which kids were born at the onset of the long dry season, resulting in very low milk yields of their dams. The latter example also illustrates that there is little point in trying to enhance reproductive performance in terms of, for instance, the number of kids born per doe exposed, as long as a reasonably high rate of survival of newborns beyond the juvenile stage cannot be guaranteed. In a similar vein, the sensitivity analysis to be presented below shows that kid survival is the single most important vital parameter determining the productivity of goat herds under the prevailing environmental conditions.

Compared to the six seasonal breeding groups, the simulated aseasonal breeding management system performed remarkably well. In terms of energetic efficiency, it ranked as the fourth best management alternative closely behind mating season group 5, and even outperformed the latter with respect to the reproductive and flock performance indices. These results were obtained by assuming that all vital and production parameters corresponded to the mean taken over all mating season groups, and that the average kidding interval in an aseasonally managed goat herd is approximately equal to 10 months. Hence, it was implicitly assumed that expected values of all vital and production parameters would remain unaffected by the increased frequency of parturitions. This type of interaction is likely to occur under semi-arid production conditions, but does not appear to have been documented in the literature. Similarly, although an average kidding interval of 10 months seems to be reasonable in view of previously reported figures (Wilson, 1992;

Wilson and Light, 1986), it is nevertheless clear that an aseasonal breeding programme is unlikely to result in a uniform distribution of conceptions throughout the year. Model parameters may therefore be misrepresented by setting them equal to expected values, averaged over all mating season groups. This is because such an approach is valid only under the assumption that the same number of does are present at the beginning of each of the six different mating periods in a year.

Principally, information on the distribution of animal abundances among the six consecutive mating periods that would be achieved if the mating season specific vital parameters were to remain constant over time can be obtained by simulating the transfer of pregnant and barren females from one mating period to another. Using data on average conception rates and kidding intervals in each mating season group, this can be done with a simple compartment model.

In order to further elucidate the effect of aseasonal breeding, such a simulation was performed by assuming that, in each mating period, does which did not conceive would be rebred in the next period two months later, while pregnant does would be bred again after 10 months, at the end of the current reproductive cycle (i.e., a constant kidding interval of 10 months was assumed, irrespective of breeding time point). Note that the effect of doe survival on the distribution was not taken into account. The structure of the model is described in Appendix 1. Based on the set of average conception rates estimated for the various mating season groups, the following relative distribution of pregnancies among the six mating periods was obtained: period 1, 17.1 percent; period 2, 15.2 percent; period 3, 17.7 percent; period 4, 17.5 percent; period 5, 16.7 percent; and period 6, 15.8 percent. Taking doe mortality into account would substantially alter this distribution, but the numerical example suffices to show that it will most likely not be uniform. Hence, the model results obtained by assuming an equal distribution of breeding females can only give a rough approximation to the level of productivity that would be achieved under aseasonal breeding management.

Although results from the aseasonal herd model have to be interpreted cautiously, there appears to be slight evidence in support of the conclusion that the increase in biological productivity associated with a shift from continuous to controlled breeding probably is much smaller than has previously been suggested. Two considerations lead to this conclusion. Firstly, seasonal breeding logically implies once-a-year reproduction, and the advantages in terms of increased reproductive and productive performance, as well as higher survival rates of kids and does, may well be offset by the higher frequency of parturitions achieved under uncontrolled breeding. Secondly, aseasonal breeding generates an unequal distribution in the number of does available for breeding throughout the year. The number of does mated in periods that lead to low biological productivity may be less than proportionate, as it was the case in the simulated distribution presented above. Hence, this effect would also tend to reduce losses incurred due to production cycles which take place under suboptimal production conditions. In this regard, generalizations are difficult to make because the distribution of breeding females at consecutive points in time within a year entirely depend on the expected value of vital parameters. Clearly, more research is needed in order to obtain data from which the biological productivity in aseasonally managed goat herds under the prevailing environmental conditions can be assessed. The final point to be made is that, as noted before, from the pastoral producer's perspective an aseasonal breeding management may generate benefits which have not been captured by the energetic efficiency criterion used to make comparisons among management alternatives. For instance, an aseasonal breeding regime may be valued for its ability to produce a constant flow of goods throughout the year, in contrast to the pulses of output occurring under controlled reproduction.

Comparison to previous productivity assessments in African goat herds

Comparison of the present productivity estimates to the results of previous productivity studies in tropical goat herds is difficult because of the lack of standardization in defining and assessing biological productivity in the literature (see Baptist, 1992*b*, for an account of the diversity of approaches that have been employed). The most widely used measures for rating the biological performance of livestock herds in the tropics still seem to be the so-called ILCA indices as defined in Wilson et al. (1985), and the modifications thereof proposed by Peacock (1987) and, more recently, by Bosman et al. (1997*a*). An attempt at comparing the performance of the goat herds studied in this work to the productivity reported for some other goat production systems in Africa is made in Table 7.8. The comparison is based on the three indices proposed by Wilson (1985), as well as on the reproductive (RPI) and flock performance indices (FPI) as defined by Bosman et al. (1997a).

Table 7.8. Productivity indices for various goat production systems in Africa

Source, breed, location		RPI	FPI	ILCA indices[1] I	II	III
• Own data [2]						
Mating season	*Scenario*					
1	Baseline	6.5	0.69	6.9	0.18	0.47
	Milk offtake	5.1	0.64			
2	Baseline	8.5	0.77	9.8	0.26	0.68
	Milk offtake	6.3	0.69			
3	Baseline	10.9	1.01	13.5	0.36	0.95
	Milk offtake	9.8	0.92			
4	Baseline	12.3	1.01	15.1	0.38	1.02
	Milk offtake	10.9	0.96			
5	Baseline	10.2	0.90	14.5	0.37	0.99
	Milk offtake	9.3	0.84			
6	Baseline	7.4	0.59	8.1	0.22	0.58
	Milk offtake	4.3	0.44			
Asea-sonal	Baseline	10.9	0.93	14.3	0.37	0.99
	Milk offtake	9.3	0.84			
• Bosman et al. (1997*a*) [3], West African Dwarf, Nigeria						
On-Station,	Unit 1	9.9	1.19	10.2		
	Unit 2	8.9	1.15	8.3		
On-farm		7.7	0.30	8.3		
• Wilson (1984)						
Sudanese Desert, Sudan				25.9		
SEA, Kenya				12.4		
Sahel, Mali				18.7		
• Wilson et al. (1985),						
SEA, Kenya				11.1	0.41	0.99
• Wilson and Light (1985),						
Sahel, Mali				14.5	0.49	1.23
• Ndlovu et al. (1996) [4],						
SEA, Zimbabwe				7.5 to 12.1		

1) IndexI=[(total Liveweight (LW) of litter at 150 days)×365/(subsequent parturition interval)]; IndexII=[IndexI/ (dam pospartum LW (ppLW) in kg)]; IndexIII=[IndexI/ (dam ppLW$^{0.73}$ in kg)].
2) RPI and FPI were transformed to annual rates and leiveweights were used instead of empty body weights; ILCA indices were computed from raw data.
3) RPI = kg LW of litter at weaning per doe and year, corrected for the time required to produce the first litter; FPI = kg net LW per kg flock LW$^{0.73}$, corrected for net inventory changes; weight of young measured at 13 weeks of age.
4) Weight of young measured at 180 days of age.

For the present experiment, ILCA indices were computed from raw, unadjusted data and are only given for the baseline scenario, since parameters for the increased milk offtake scenario were derived from statistical models fitted to the same data. ILCA productivity indices were calculated on the basis of individual observations per female breeding animal. Does whose litters died before weaning (or before reaching the time-endpoint at which weights used in calculating in the index are measured) are usually taken into account by setting their productivity indices to zero (Wilson et al., 1985), and this was also the procedure adopted here. Values for the reproductive performance (RPI) and flock productivity indices (FPI) by mating season were transformed to annual rates and calculated in terms of live weights instead of empty body weights so as

to allow comparisons to be made to the results reported by Bosman et al. (1997*a*). (Note that corrections for the time required to produce the first litter and for net inventory changes as made by these authors were not necessary in the present study, because these adjustments were implicitly made by imposing steady-state herd size and structure).

Table 7.8 shows that in terms of reproductive performance (RPI) the results for the baseline scenario are comparable to the values reported by Bosman et al. (1997*a*) for West African Dwarf goats. However, the figures for the best performing mating season groups (3 to 5, and aseasonal) tended to exceed those observed in the latter study. The picture is reversed when comparisons are made on the basis of the flock productivity index (FPI), probably due to the lower mature weight of the West African Dwarf goats. In this case, does of the West African Dwarf breed that were kept on-station outperformed the mating season 4 flocks by about 14 to 18 percent. The figures for the milk offtake scenario clearly indicate that, as noted before, the use of RPI and FPI should be limited to productivity ratings in single-product, meat production systems, since they cannot account for production benefits other than meat or live animals. Although not computed for the increased milk offtake scenario, a similar negative bias in the performance of dual-purpose herds would also occur if comparisons based on the three ILCA indices were to be made.

With respect to the ILCA index I, the figures calculated for mating season groups 3, 4, 5, and the simulated aseasonal reference herd exceeded that recorded for SEA goats in southern Kenya (Wilson, 1984; Wilson et al., 1985) and in Zimbabwe (Ndlovu et al., 1996). As before, the relationship was reversed when doe liveweight was used as the denominator (indices II and III). With respect to index I, the Sudanese Desert goats studied by Wilson (1984) appear to be far more productive than all other production system and breed combinations included in Table 7.8. However, it should be noted that in addition to the failure to account for products other than meat and live animals, the indices employed in Table 7.8 do not adequately correct for feed availability and/or differences in mature size. In this respect, Ogink (1993:6) points out that the practice of using the breeding female's liveweight as the denominator in productivity indices tends to overvalue small individuals because their production level per unit weight is higher as a result of their smaller size. Hence, with regard to their use for comparative purposes, these indices cannot be expected to provide reliable estimates of the biological production potential of different breeds maintained under the same environmental and managemental conditions, or of the same breed maintained under either different environmental conditions, different management systems, or combinations of both factors. Based on these grounds, the statement made by Wilson (1984: 251) that the Maasai herders of Kenya "show results greatly inferior" to the husbandry systems in Sudan and Mali appears to be unsubstantiated, since the ILCA index I utilized in this report corrects neither for differences in mature size between breeds nor for differences in available feed resources between the three husbandry systems. As pointed out by James and Carles (1996), comparisons of productivity among different production systems are likely to be very misleading if they do not take into account differences in feed inputs.

Optimum decision rules

A close relationship has been found between flock performance in terms of energetic efficiency on the one hand, and asymptotic growth rate and net reproductive rate of the flock on the other. Similarly, the calculated measure of flock performance (FPI) and of reproductive performance (RPI) appeared to be an increasing function of asymptotic population growth (Fig. 7.11). Thus, for a given range of alternative management strategies, each described by a specified herd projection matrix, it would seem that the strategy corresponding to the projection matrix with the largest dominant eigenvalue (λ) will also tend to be the one for which biological efficiency of the herd is highest under optimal culling. Interestingly, qualitatively similar relationships are often supposed to hold true with regard to the selection for optimal life histories in natural populations. For example, a fundamental assumption of research conducted in the field of life-history theory is that each life-history strategy can be characterized by its population growth rate (λ), and that natural selection usually leads to a strategy which maximizes this growth rate, or average fitness of a population (Caswell, 1980, 1982; de Kroon et al., 1986; Houston and McNamara, 1992; McNamara, 1993).

Figure 7.11 also shows that the apparent equivalence between the management strategy (i.e., the optimum choice of mating season in the present context) which maximizes energetic efficiency and that which yields the largest rate of herd growth per time unit is not affected by an increase in milk output for human consumption. This suggest that, at least for this type of goat production system, the major factors determining biological productivity pertain to vital rates (i.e., fecundities, survival, and developmental rates), and not yield levels (i.e., growth and lactation performance). Hence, a tentative conclusion would be that a simplified herd productivity assessment procedure could consist of ranking alternative management strategies or production systems according to their associated asymptotic population growth rate. The information required to carry out such an assessment reduces to the sets of survival, developmental, and fecundity patterns generated by the different alternatives. It should be emphasized, however, that the equivalence

between the most biologically efficient alternative and that which produces the largest long-term population growth rate is conditional upon implementing a stage-specific optimal culling policy which maximizes energetic efficiency, subject to keeping herd size and structure constant over time. The possibility of increasing yields through stage-selective culling has been demonstrated by comparing model results to a proportional culling regime which removes equal fractions from each stage group. Essentially, this finding may be regarded a standard result from optimal harvesting theory in age- and stage-structured populations. Mathematical proofs of the superiority of age- or stage-selective harvesting policies over proportional ones are provided by, among others, Beddington and Taylor (1973), Doubleday (1975), Reed (1980), and Rorres (1976). Beddington and Taylor (1973) and Doubleday (1975) also point out that this superiority is preserved irrespective of whether the objective functional is expressed in terms of number of animals or some other yield, for example body weight, biomass, economic value, or any linear combination of the proportions harvested from the separate groups.

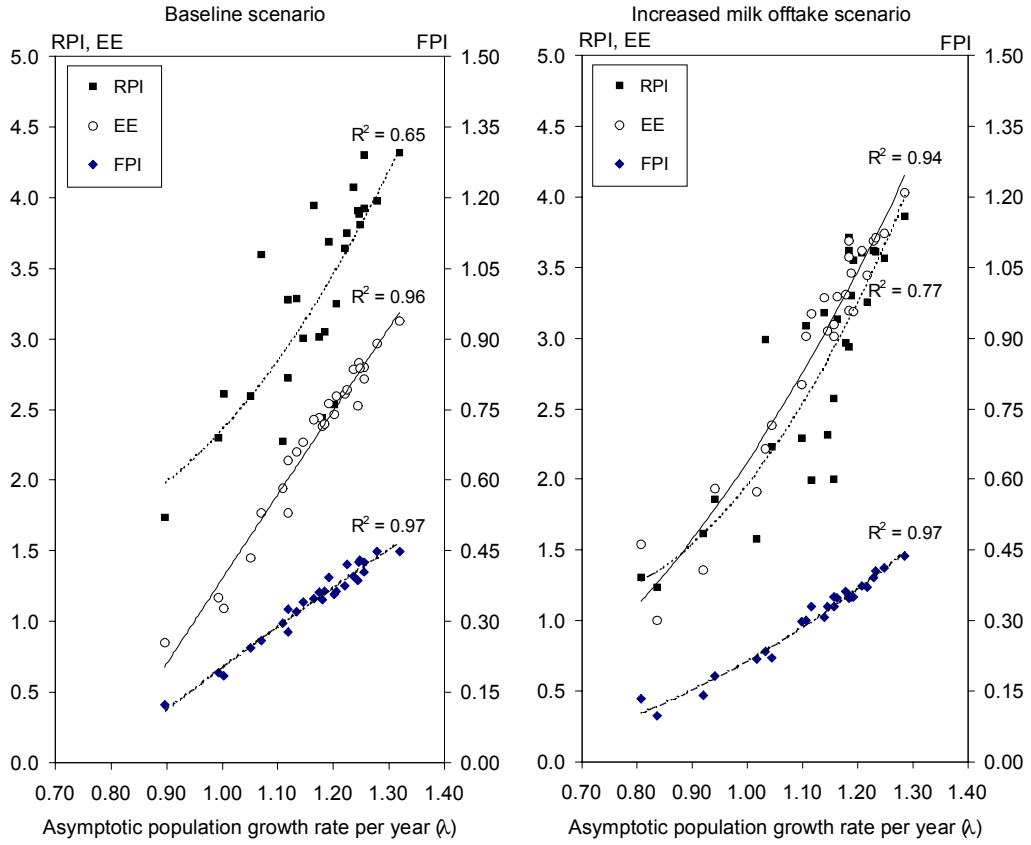

Figure 7.11. Relationship between asymptotic population growth rate (λ) and energetic efficiency (EE), reproductive performance (RPI), and flock performance (FPI). Second-order polynomials in λ were used to fit trendlines. The plots are based on the results from the productivity assessments for all mating season×production cycle combinations, including results for the aseasonal reference group as well as for the seven "average" model runs.

At first sight, offtake rates exceeding potential population growth per time unit, as presented in this study, may seem to be unrealistic. However, this is only true when an equal proportion of animals is to be removed from all stages, thus leaving overall herd *structure* unchanged from one time period to the next. In contrast, non-proportional culling policies such as those shown in Table 7.3 do affect herd structure and, by shifting relative abundances in favour of the most productive stages, herd growth. The effect of stage-selective culling upon population growth is perhaps best illustrated by looking at the relative increase in herd size over the first projection time period when a herd previously driven to equilibrium size and structure through optimal culling is suddenly allowed to grow unrestrictedly. These figures can be calculated by postmultiplying the transition matrix **A** by the stable stage distribution vector n^* from the herd productivity assessment procedure (equation (25)), so as to obtain a new stage distribution vector n'. n^* and n' can then be used to calculate the relative increase in herd size after removing management controls. For example, the first-step increases in herd size calculated for the "average" models of mating season groups 1 and 4 and the aseasonal reference flock were, respectively, 14.1, 23.1, and 19.6 percent, while the corresponding

asymptotic rates (λ), to which the rate of herd increase would have decayed subsequently, were much lower at 4.6, 8.3, and 7.6 percent. This suggests that maximisation of herd energetic efficiency through optimal culling implicitly maximizes the rate of self-renewal of the herd. Indeed, in studying harvesting patterns that maximize the yield per recruit in age-structured populations, Gray and Law (1987) were able to show that, usually, yield is maximal when the self-renewal of the culled population is at its greatest.

In the present setting, this meant that all available female youngstock were used as replacements. In terms of energetic efficiency, it was never profitable to keep female youngstock as surplus for fattening. Instead, model predictions indicated that it should always be more advantageous to exploit their reproductive potential and, hence, their capacity to contribute to future herd growth and to the production of surplus male animals, before using them as a source of energy output from the system. Of course, optimal decision rules may be radically different when productivity assessments are based on criteria other than energetic efficiency, and when prevailing market demand and prices for livestock products, as well as resource constraints within the herding enterprise are taken into account. This does, however, neither invalidate the results, nor the general approach to livestock productivity assessment presented in this work. To the contrary, the procedure presented is perfectly amenable to incorporating such extensions and to carrying out a full, economic activity analysis of livestock operations.

It should be emphasized that other available procedures to steady-state productivity assessments in livestock herds such as those proposed by James and Carles (1996) and Upton (1993), would not have been able to arrive at decision rules similar to those presented above, since these procedures determine offtake rates, and thus optimal herd structures, as residuals *after* all replacements necessary to maintain herd size constant over time have been made. This approach to steady-state modelling invariably generates decision rules which (in order to maintain herd size constant) use only part of the newborn females for breeding, and which do not fully exploit the potential for increasing herd productivity through actively manipulating herd structure. Very different predictions with regard to the biological efficiency of livestock herds may thus result when using the procedures proposed by the previously cited authors.

With respect to optimal culling stage for fertile breeding females, different rules emerged depending on potential herd growth rate. In herds with potential rates of increase per year in excess of 18 percent (mating seasons 3, 4, 5, and the aseasonal reference flock), maximum energetic efficiency was achieved when breeding females were culled after their third lactation. This may seem somewhat surprising, because third parity does were predicted to have the highest fecundity rate, irrespective of mating season. However, there is a trade-off between reproduction and survival of does over consecutive production cycles, such that a higher efficiency is attained by culling does at an earlier stage, even though there is some loss of reproduction. In contrast, for herds with insufficient growth potential due to high kid and/or doe mortality (mating seasons 1, 2 and 6) culling policies had to be adjusted so as to meet the steady-state constraints, and does tended to be kept in the breeding herd at least until they had completed their fourth lactation. Optimal culling policies for nonconception showed similar differences between mating season groups as those described for fertile breeding females. In herds with adequate growth potential and seasonal mating, does were culled immediately after failure to conceive, irrespective of parity stage (mating seasons 3, 4, and 5). In contrast, with decreasing availability of female replacements, temporarily infertile first-breeders were at least kept until the next mating season one year later (mating seasons 1, 2 and 6). Finally, when the frequency of breeding was increased (aseasonal herd), the expected energy yields generated by a successfully established pregnancy tended to outweigh the energetic costs associated with maintaining a nonpregnant breeding female until the next breeding event, such that reproductively inactive does with at most one prior kidding were given the chance to breed at least for one more time. Similarly to the pattern described for mating season groups 3, 4, and 5, all nonconceiving higher parity does were immediately culled in the aseasonal reference herd.

An interesting pattern emerged with respect to optimal culling ages for surplus male animals, in that these appeared to depend upon the level of energetic efficiency achieved in the breeding herd. Generally, optimal culling ages increased with decreasing productivity of the breeding herd, which itself was determined by fecundity and survival parameters. Note that this was possible due to the fact that the optimization model employed did not constrain the available quantity of forage, but only the total size of the herd. Although this assumption seems to be unrealistic, it has nevertheless been stated previously that standing biomass on semi-arid rangelands in Kenya often is not the primary limiting factor for livestock production, but rather the low levels and digestibility of energy and crude protein (Pratt and Gwynne, 1977; Western and Finch, 1986). If the simplifying assumptions underlying the present productivity assessment procedure are accepted, the decision rules it generates seem to contradict the common belief that, in order to assess overall herd productivity, surplus animals (males and females), and breeding females and their replacements can conveniently be considered as two separate herds (Matthewman and Perry, 1985). This is mostly based on the argument that gains and losses from surplus animals do not affect the productivity of the breeding female herd, and that inefficiencies in the breeding female herd have an effect on the surplus herd only through the number of youngstock available for fattening, and possibly through less than optimum growth rate due to

insufficient milk production. It is further assumed that maximum biological productivity can be achieved upon optimizing these individual components separately. However, the results of the present study clearly showed that the assumed separability between individual herd components may not hold, and that the optimal culling age for surplus animals may depend upon the level of energetic efficiency achieved in the breeding herd. The main reason for this is that indices of biological productivity are intrinsically non-linear (and thus nonadditive) in nature, since they represent ratios of outputs to inputs. Hence, overall (optimum) herd productivity must be determined by simultaneously choosing appropriate culling ages/stages for both surplus and breeding animals, and by summing all outputs produced and inputs required in the production process prior to calculating productivity measures.

The consequences of ignoring these relationships may be far reaching, as illustrated by an interesting example from animal breeding reported by Ogink (1993: 4). In broiler production, animals have for long been selected for high growth rate, high feed efficiency and high lean proportion at a fixed slaughter weight. This has favoured the selection of large sized animals, since, at equal weight, larger sized animals are physiologically less mature and thus tend to display a faster growth rate, higher feed efficiency, and higher lean proportion than genetically smaller sized (and thus more mature) animals. However, this breeding strategy has also led to very large sized parental stock which is expensive to maintain in terms of feed energy consumption and thus has a depressing effect upon overall energetic efficiency. If the breeding strategy would have been based on an evaluation of overall energetic efficiency of the production process, instead of exclusively focusing on the surplus animal part of it, breeders probably could have avoided these negative effects by defining size-independent selection traits for improving feed efficiency and lean proportion.

With regard to the comparison of optimal culling ages of surplus male animals between mating seasons 1 and 4, it is worth noting that the much higher optimal culling age in mating season 1 is entirely due to the suboptimal performance of the breeding female herd, and not to low productivity of the surplus male herd, as indicated by the plot on the left of Figure 7.7. Energetic efficiency of the breeding female part of the herd is impaired by excessive kid and doe mortality rates, which lead to a shortage of female replacements. Consequently, there is also little scope for improving herd structure, and, by this means, herd reproductive rate through stage-selective culling. In conclusion, situations such as those characterized by herds pertaining to mating season 1 may provide a rational explanation for the often observed phenomenon that 'unproductive', i.e., older surplus animals, are kept in pastoral flocks. This may be a complementary motive to that of insurance or financing (Bosman et al., 1997), though it would require the assumption that, principally, pastoralist producers aim at maximizing energetic efficiency of their goat herds.

Production risk

The major risk faced by pastoral producers in semi-arid areas is the considerable variation in yields obtained from livestock. This variation is primarily of climatic origin, which not only causes large seasonal fluctuations in the availability of production resources, but also leads to large differences in seasonal resource availability between individual years. The unpredictability in yields faced by pastoral producers will necessarily affect their decision-making process and, hence, their herd management strategies. As has been stated previously by Mace and Houston (1989), the most rational option for pastoral households operating in unpredictable environments appears to be the maximisation of their long-term viability. Clearly, then, evaluating improvements to existing management practices must take into account both the mean level of output, as well as the variability in output generated by individual management alternatives. Additionally, in agricultural production, risk (or variation) is now often identified as the most important factor in the adoption process of new technologies and management practices (Anderson et al., 1977; Anderson and Dillon, 1992), such that this aspect deserves special attention.

In the present work, production risk was described in terms of coefficients of variation pertaining to individual herd productivity measures (Tables 7.2 and 7.6). In light of the importance of the subject, this is a rather cursory treatment, and a more elaborate approach building upon the proposed procedure for herd productivity assessments will be discussed further below. Nevertheless, results of the baseline scenario indicated that the best performing seasonal mating groups also displayed the lowest variability in productivity as measured by energetic efficiency or FPI (groups 3, 4 and 5). With respect to RPI, rankings were somewhat different, because of the strong influence of early kid growth and survival on this index. On the basis of the present results, the hypothesis that restricted breeding entails an increased variability in pastoral goat herd productivity has to be rejected. The aseasonal reference herd showed a fairly large variability in energetic efficiency of 23.1 percent, compared to only 12.8 percent for the best seasonal breeding group 4. Since the aseasonal model was constructed from mean parameter values taken over all mating season groups, the large variability in performance observed in some of the mating season groups was in part carried over to the aseasonal reference herd. Clearly, joining does in the period from December to April has substantial negative impacts on both the predicted level of, and the variability in, productive efficiency. The main reason for the

large variation in energetic efficiency of mating season groups 1, 2, and 6 is that their productive performance was highly dependent upon good forage availability towards the end of the long rainy season, a period during which moisture supply and thus pasture forage production is particularly unreliable.

The change in the production system as simulated by the increased milk offtake scenario did not affect the rank orders of the various management alternatives with respect to variation in performance indices. There was some evidence that the shift to a dual-purpose production system might reduce variability in goat herd performance at high levels of energetic efficiency (mating season groups 3 and 4), despite the negative impact of an increased milk offtake for human consumption on kid growth and survival. Similarly, although a relatively large inflation of kid mortality occurred in some of the mating season groups (groups 1, 2, and 6) due to the reduced milk availability until weaning, increases in the coefficients of variation of energetic efficiency were relatively small when compared to the results of the baseline scenario. This indicates that the more efficient conversion of feed energy to milk as opposed to liveweight may have a buffering effect on overall herd productivity.

As indicate above, describing variation in terms of coefficients of variation may be considered an inadequate assessment of the inherent variability attached to individual management alternatives. Like sensitivity analysis, coefficients of variation which were computed from a rather small number of observations (two for mating season group 6, and three for all other groups) present a very limited view of the wide range of possible outcomes for each management alternative. More formal methods of risk analysis, such as stochastic dominance analysis, are available which provide more insight into the 'riskiness' of management alternatives. Generally, formal risk analysis methods involve the specification of probability distributions of uncertain or stochastic variables that are deemed to have a major effect on outcomes of interest, (i.e. herd productivity in the present context) in order to generate (cumulative) probability distributions of outcomes for each of the considered decision alternatives. This is usually done by simulating or calculating (for each alternative) outcomes of the performance measure for a large number of possible combinations of values for the stochastic variables. The outcome distribution itself already constitutes valuable information which can be used to compare decision alternatives based on criteria such as: mean, variance and range of the performance measure; the probability that the performance measure takes on specific values, or that it either falls below or exceeds certain critical thresholds. Alternatively, risky decision alternatives can also be compared in terms of full *distributions* of outcomes, not just in terms of moments, using stochastic dominance analysis (Hardaker et al., 1997). Stochastic dominance analysis is intended to be used for ranking decision alternatives in situations where the preferences of the decision maker cannot be elicited and described. Based on increasingly stronger assumptions concerning the decision-makers preferences (i.e., the decision-maker has positive marginal utility for the performance measure and is risk averse) stochastic dominance criteria of varying degree can help in identifying a risk efficient set of decision alternatives. A full treatment of stochastic dominance analysis is given in Hardaker et al. (1997). The essential prerequisite for the mentioned methods of risk analysis is to generate a probability distribution of the performance measure under each management alternative. In what follows, a short description is given on how such a distribution could be generated within the framework of the productivity assessment procedure proposed in this work.

Principally, one can apply resampling techniques such as bootstrapping to construct distributions of the vital rates (conception, fecundity, and survival rates) and yield levels (milk and growth performance traits) for each of the mating season treatments. Two different ways of obtaining bootstrap distributions for these parameters are available (Neter et al., 1996). The first procedure obtains bootstrap replicates of predicted values of all required vital rates and production parameters directly from the estimated models by adding randomly sampled residuals to the predicted values. The other is to randomly select individuals for a number of m samples, and to fit the same statistical models m times using these samples to the individual traits, such as was done in this study for obtaining confidence intervals of survival curves. The latter is the only practical way, since we need to obtain estimates for all traits from a common sample. In the first place, then, this approach requires sampling a number m of new bootstrap data sets from the original experimental data for each of the 17 breeding groups. Note that the bootstrapped data sets must be drawn from the original data set according to the original sampling design (McPeek and Kalisz, 1993). The m different estimates obtained for each trait and mating season could then be utilized to parameterise m different herd productivity assessment models for each treatment group. Although the general procedure for generating the bootstrap distribution of performance measures is relatively straightforward, the computational burden involved to obtain a large number ($m \approx 100$) of bootstrap estimates for each model parameter and solving the same number of non-linear optimization models can be quite formidable. In the present context, it would be impossible to carry out the individual steps manually, and the entire procedure would need to be automatised by programming it using, for example, the SAS programming language. An advantage of using the SAS-System is that both the required statistical as well as the non-linear optimization routines are provided as built-in procedures.

Chapter 8

General discussion

The present work examined the joint impact of environmental seasonality and controlled breeding on biological productivity of pastoral goat herds. To this end, a field experiment was conducted over a period of three years under simulated pastoral management conditions on a semi-arid thornbush savannah in northern Kenya. The experiment provided data on relevant biological performance traits of seventeen breeding groups for a total of 381 exposures distributed among six consecutive mating seasons each of two months duration, so as to achieve year-round mating, kidding, and weaning. In terms of both its design and degree of detail of data collected, the present experiment differed markedly from those conducted previously on the same subject. For instance, a total of 8547 recordings were made on survival, liveweight, and milk production of does, while survival and liveweight development of youngstock were measured at a total of 9837 time points. Also, recordings extended over entire production cycles until youngstock had reached at least the yearling stage.

Most previously published studies did not involve the experimental imposition of restricted breeding as an external treatment factor on experimental animals, but merely made use of data gathered for a wide variety of other purposes to retrospectively investigate the effects of environmental seasonality on biological performance. To this end, observations on individual animals were often grouped into several breeding or kidding seasons prior to statistical analysis. Examples of this approach with respect to goat production include: the studies on milk yields by Kennedy et al. (1980), Ruvuna et al. (1995), and Montaldo et al. (1997); the studies on reproductive performance conducted by Wilson et al. (1984), Amoah et al. (1995), Mellado et al. (1996), Ndlovu and Simela (1996); the reports on liveweight development by Wilson et al. (1984), and Ruvuna et al. (1991). To the best of our knowledge, in the context of African pastoral husbandry systems, the present study is the first attempt to investigate the biological consequences of confining breeding in goat herds to a short period in a year through the implementation of a planned and systematic breeding programme. For obvious reasons, in order to answer such complex questions as the biological consequences of seasonality, experiments are generally to be preferred to non-experimental or observational approaches in which the investigator cannot apply treatments to the animals under study and has limited control over data collection. The main problem associated with the latter approach is that causal explanations become problematic and are generally less convincing than in the former approach, which allows conclusive statements to be made on the sampled population (Hurlbert, 1984; Jager and Looman, 1995). Additionally, unplanned analyses of differences or relations perceived in the data have detective value only in the sense that the scope of inference is limited to the target population actually studied, but cannot be extended to the population at large, or inference space, implicit in the hypothesis being tested. With respect to the literature reviewed in the course of this work, these kinds of problems are most evident in relation to published results on the effects of environmental seasonality on the reproductive performance of goats. Due to their observational design many previous studies were unable to measure component traits of reproduction such as conception and prolificacy rate, and instead assessed reproductive performance in goats in terms of compound indices. This type of approach may obscure real explanations for detected differences in measured or derived variables, because underlying factors have not been measured. Compelling evidence for the presence of such confounding comes from the study of Wilson et al. (1984, 1985), who found individual flock ownership to have a large impact upon reproductive performance and overall herd productivity of Maasai goat herds.

Despite the clear-cut treatment structure adopted in this study, statistical analysis of the data and interpretation of results was complicated due to deficiencies in the design structure of the experiment. These were mainly caused by resource constraints, particularly with respect to the availability and homogeneity of experimental units, i.e., breeding does. For example, it would have been beneficial to achieve a more homogeneous repartition of does across liveweight and parity classes in each of the breeding groups. This would have facilitated studying differential effects of parity within liveweight classes on various traits, particularly on those pertaining to reproductive performance. Also, the sensitivity of the analysis could have been increased by assigning a maximum number of animals repeatedly to the same mating season over the three consecutive reproductive cycles. The problems caused by resource constraints were further exacerbated by the longitudinal nature of the study, in that experimental animals were lost to follow-up due to mortality or other reasons, thus creating additional imbalances in the design structure of the experiment. This, however, is a feature common to many longitudinal studies. Typically, individual animals are observed a different

number of times, at different periods of time, and the intervals between observations may be different as well. On the other hand, all production traits can be considered to be measures of performance over time and, although cross-sectional approaches are conceivable, the most reliable estimates of performance traits are generally obtained by precisely adopting a longitudinal or repeated measures type of study design.

In this regard, the general and generalized mixed model approaches used in analysing all traits, except for kid and doe survival, proved to be particularly advantageous. Firstly, it allowed the taking into account of the between-subject variability, of variability among production cycles, or both. For most traits analysed, at least one of these random effects were found to account for a significant part of the observed variation, and the analyses could be made more sensitive by removing them from the error term. Secondly, a method of analysis which allows modeling more than one error term was required because repeated measures on the same experimental animals are not independent, and cannot be analysed as if they were. The mixed model approach is a particularly effective technique to control the variability among responses from different experimental units and at the same time to account for the positive correlation between any two measurements on the same unit. A direct consequence is that the linear mixed-effects model leads to more precise estimates of outcomes for factors of interest, while it readily accommodates for the high unbalancedness typical of longitudinal data. The most commonly used method of analysis, which involves carrying out an ANOVA of the data at each time point separately (i.e., the so-called time-by-time ANOVA), provides no tests of the change of treatment effects with time and thus are generally less powerfull relative to the mixed model approach. Since treatment effects tend to vary continuously over time, quoting the time at which an effect becomes significant has very little relevance when using time-by-time ANOVA (Rowell and Walters, 1976). In the last decade, significant progress has been made in the development of methods appropriate for the analysis of longitudinal data. As these methods are now widely accessible to applied scientists, using suboptimal techniques like time-by-time ANOVA would seem unacceptable (von Ende, 1993).

In much the same way, analysing non-normally distributed outcomes such as survival rates with conventional ANOVA or linear regression methods should be avoided. With respect to survival data, the present work has shown that standard logistic regression is a particularly flexible and easy to use method of analysis which can be employed to model hazard functions parametrically over time. The proposed method provides insight into patterns of mortality over time and allows comparison among any number of risk groups simultaneously at any time point. Typical features of time-to-event data such as censoring, changes in the risk set over time, and time dependent covariables can be accommodate for, which is not possible with conventional approaches usually adopted in livestock-related research.

The results of the statistical analysis indicated that parity stage of breeding females is an important factor affecting various aspects of reproductive performance in goats. In this respect the present study concurs with many previous ones conducted on the same subject. Mating season, however, was not found to have a statistically significant effect on reproduction traits, although this does not necessarily preclude its biological significance. Numerically, the range of predicted values for traits such as conception and prolificacy rates among mating seasons were quite large, but the variability in within-season environmental conditions among the three production cycles was too high to permit clear expression of statistical differences in these measures. In general, however, maximum reproductive performance in goats kept on semi-arid pastures in northern Kenya can be expected to be achieved when does are mated during the short dry season in January or February. But, at the same time, this management strategy would lead to very large mortality rates in youngstock, so that in terms of the number of kids weaned the best performance would be obtained if mating took place during and towards the end of the long dry season, so that birth and weaning coincides with the long rains and the beginning of the following long dry season, respectively. Differences in kid survival among mating seasons were marked, particularly between the latter mating season group and those in which breeding took place between the months of December and February. The results demonstrated that restricted breeding can be an effective means to manipulate kid mortality. Similar conclusions apply with respect to milk yield, which was an important risk factor affecting kid survival until weaning. Although growth performance of kids until weaning differed markedly among mating seasons, these had largely disappeared by one year of age. Therefore, seasonal breeding does not seem to confer any major advantage in terms of growth performance of youngstock per se. However, account should be taken of the fact that juvenile developmental rates have an impact on survival rates, especially in the early stages of life, and thus affect the expected total liveweight production of youngstock per time unit.

One of the major conclusions that emerged from the herd productivity assessment is that under the current production conditions reproductive performance traits are far less important as contributors to biological productivity than is often assumed. This is due to two main reasons. Firstly, if juvenile mortality is high, resources invested in producing offspring, i.e. in maintaining reproductively active breeding females, are wasted, and therefore youngstock mortality will tend to outweigh reproductive performance traits in its effect on biological productivity. The results of the eigenvector sensitivity analyses carried out on the transition

matrices for each mating season group clearly supported the contention that juvenile survival rate is the most important factor determining overall energetic efficiency. Secondly, in order to assess the contribution of individual traits to, or the effects of changes in, individual traits on herd efficiency their impact on the entire production process, particularly on herd dynamics, must be considered. This can be difficult to achieve with conventional production indices on which most comparative studies have relied, while it is explicitly taken into account by the steady-state herd model proposed in this study. The distortions in rank orders which may emerge from an analysis carried out on the basis of conventional production indices may be substantial.

To summarize, the general impression that emerges from this study is that restricted breeding can effectively be used as a management control to manipulate overall biological herd productivity primarily because of its positive effect on youngstock mortality rates. In contrast, yield levels, i.e., growth and milk performance, are less important as determinants of biological herd productivity, once their effect on youngstock mortality has been accounted for. Ultimately, this is the main reason for the strong positive relationship that was detected between energetic efficiency and asymptotic herd growth rate. Therefore, an interesting suggestion arising from this part of the study is that a simplified productivity ranking of goat herds maintained under similar environmental and management conditions could be carried out on the basis of asymptotic growth rate, for which only stage-specific vital rates for each alternative considered need to be known.

The results of the increased milk offtake scenario re-emphasized the statement that has frequently been made before by ecologists, namely that the combined production of meat and milk for human (subsistence) consumption confers a distinctive advantage over the specialised single-purpose meat production usually found in commercialised extensive livestock production systems. The ranking of mating season groups was little affected by the change in production strategy; rather, in both the baseline and the increased milk offtake scenario, joining does at the peak of the long dry season proved to be the optimal management strategy. However, whether restricted breeding is biologically superior to an aseasonal breeding management, as is often practised by pastoral producers, remains an open question. The results of the productivity assessment for the simulated aseasonal breeding regime seemed to indicate that the potential improvements in biological productivity that could be realized by shifting to a controlled breeding regime are perhaps much smaller than is usually presumed. But, clearly, this conclusion needs to be confirmed by additional empirical evidence. Furthermore, it should be kept in mind that controlled breeding requires a much higher standard of management than those currently being practised by many pastoral producers. This points to the fact that although assessing productivity in biological terms is a necessary step because its components are also important determinants of economic efficiency, it is not sufficient for a final rating of management alternatives. Priority for further research should therefore be placed, firstly, on obtaining more reliable estimates of biological productivity in aseasonally reproducing pastoral goat herds. Secondly, socio-economic studies of pastoral livestock operations are required in order to quantify the economic benefits associated with restricted and unrestricted breeding management. Because of the complex interrelationships between decision making at the herd and at the pastoral household level, such studies should be based on a comprehensive and formal analysis of the objectives of pastoral producers.

Carrying out additional experiments to test the hypothesis that biological productivity of continuously reproducing SEA goat herds is lower than that achieved when breeding is restricted to the long dry season would also offer the opportunity to investigate the effects of changes in age at first breeding and kidding interval on energetic efficiency. Management interventions aimed at reducing both of these variables in goat herds have often been stated to lead to significant improvements in overall biological efficiency, although so far little effort has been put into quantifying these benefits. In order to achieve comparability to the present results, the suggested experiments should, at the very least, take place under similar environmental and management conditions, and the age-at-first-breeding treatment variable should include as a reference level an age of about 15 months, which corresponds approximately to that observed in the present experiment. Based on the results of the sensitivity analyses performed in this work, it may be hypothesised that the effect of kidding interval on energetic efficiency will depend on the age at first breeding and *vice versa*, such that a two-way-factorial treatment structure appears to be warranted.

With respect to the assessment of biological productivity at the herd level, the methodology developed in the present work is basically an extension of the approach proposed by Baptist (1992*b*). While the latter assumes that the same inherent survival, fecundity, development rates, as well as yield levels are applied to all breeding and (except, of course, for fecundity rates and milk yields) surplus females alike, the stage-structured population dynamics model employed here is much more flexible since it permits the modelling of life histories in which vital rates, growth and milk performances vary with age, stage, or a combination of both factors. Generally, the appropriate definition of relevant life-cycle stages is entirely dependent on the species and on the production context considered, and is not limited to the parity stages that were used in modelling population dynamics of SEA goat herds. Perhaps most importantly, the present work has demonstrated that assessing biological herd productivity can be formalised in a non-linear programming model which determines the optimal stage-specific culling policy that maximizes the chosen biological or

economic productivity criterion, subject to the constraints that herd size and structure remain constant.

The present work has emphasized the importance of utilizing an optimality approach for obtaining a common basis on which management alternatives can be compared in terms of their effect on energetic efficiency. Many other approaches to steady-sate herd productivity modelling, such as that of James and Carles (1996) and Upton (1989, 1993), are based on *estimated* offtake rates for a given management alternative or production system and do not attempt to simultaneously optimise herd structure and offtake rates in order to maximize a specific performance criterion. The results of this study have shown that herd productivity is greatly affected by the choice of culling policy and thus herd structure. Of course, herd management affects herd productivity not only through offtake decisions but, if potential herd productivity is to be assessed, at least this major source of variation should be controlled for in comparative assessments. The reason for this is that productivity assessments may be biased if they are based on observed, suboptimal offtake decisions.

The herd productivity assessment procedure developed in this work should be seen as a device with which standardized comparisons of productivity in livestock herds can be carried out. As was illustrated by the results of the sensitivity analyses, steady-state herd productivity models of this type can also be a valuable aid in understanding or optimising the production system looked at. The required input data can either originate from field experiments or livestock surveys, but can as well be generated by simulation models of livestock production systems such as the one described by Bosman et al. (1997*b*). With regard to simulation experiments, steady state herd productivity modelling can represent an important complementary step in evaluating simulation results. For example, in a simulation experiment, Bosman et al. (1997*b*: 570) assessed goat herd productivity in terms of RPI and FPI, and argued that productivity indices may be seriously affected by adult liveweight if the amount of some or all feeds available may be limited. This problem occurs mainly because RPI and FPI do not qualify as true measures of biological productivity. Differential effects of adult liveweight on efficiency through variations in the intake above maintenance and, hence, through restrictions in herd size could easily be assessed through steady-state herd productivity modelling with energetic efficiency as the objective criterion. Upon using the approach presented in this work and introducing an additional constraint with respect to total feed energy consumption into the non-linear programming model, one could explicitly take into account differences in mature size (and thus in inputs required and outputs produced) and obtain undistorted estimates of biological productivity at the herd level.

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Appendix 1

This Appendix describes the structure of the simulation model used to assess the effect of an aseasonal breeding regime on the distribution of pregnancies in goat herds throughout the year. The assumed length of kidding interval was 10 months. Doe mortality was not taken into account. The flow from one mating season (MS*n*, *n*=1,...,6) to another is a function of the observed conception rate (ConRateMS*n*) in each mating season group. Exposed females that failed to conceive (BarrenMS*n*) were assumed to be re-bred during the immediately following mating period (i.e., two months later). Pregnant females (ConMS*n*) stay for 10 months in the reproductive cycle (RepCycleMS*n*) before making the transition (NextBreedingMS*n*) to the next mating period.

The model was implemented with the graphical simulation software STELLA, Version 5.0 (High Performance Systems Inc., Hanover, 1997). The model-diagram is depicted in Figure A.1. The model equations are given below. Note that a bi-monthly simulation time step was used. The simulation run started with an initial population of 1000 does in MS1, and 0 animals in all other states. The model converged to the following stable distribution, independently of the initial state distribution of 1000 animals choosen:

State (***n***=1,...,6)	1	2	3	4	5	6
Mating season [MS***n***]	34.6	35.9	40.3	38.4	35.1	35.8
Reproductive cycle [RepCycleMS***n***]	133.3	118.6	138.2	136.4	130.4	123.2

State Variables and flows

```
MS1(t) = MS1(t - dt) + (NextBreedingMS2 + FailConMS6 - FailConMS1 - ConMS1) * dt“
INIT MS1 = 0
INFLOWS:
    NextBreedingMS2 = CONVEYOR OUTFLOW
    FailConMS6 = (1-ConRateMS6)*MS6
OUTFLOWS:
    FailConMS1 = (1-ConRateMS1)*MS1
    ConMS1 = ConRateMS1*MS1

MS2(t) = MS2(t - dt) + (NextBreedingMS3 + FailConMS1 - FailConMS2 - ConMS2) * dt“
INIT MS2 = 1000
INFLOWS:
    NextBreedingMS3 = CONVEYOR OUTFLOW
    FailConMS1 = (1-ConRateMS1)*MS1
OUTFLOWS:
    FailConMS2 = (1-ConRateMS2)*MS2
    ConMS2 = ConRateMS2*MS2

MS3(t) = MS3(t - dt) + (NextBreedingMS4 + FailConMS2 - FailConMS3 - ConMS3) * dt“
INIT MS3 = 0
INFLOWS:
    NextBreedingMS4 = CONVEYOR OUTFLOW
    FailConMS2 = (1-ConRateMS2)*MS2
OUTFLOWS:
    FailConMS3 = (1-ConRateMS3)*MS3
    ConMS3 = ConRateMS3*MS3

MS4(t) = MS4(t - dt) + (NextBreedingMS5 + FailConMS3 - FailConMS4 - ConMS4) * dt“
INIT MS4 = 0
```

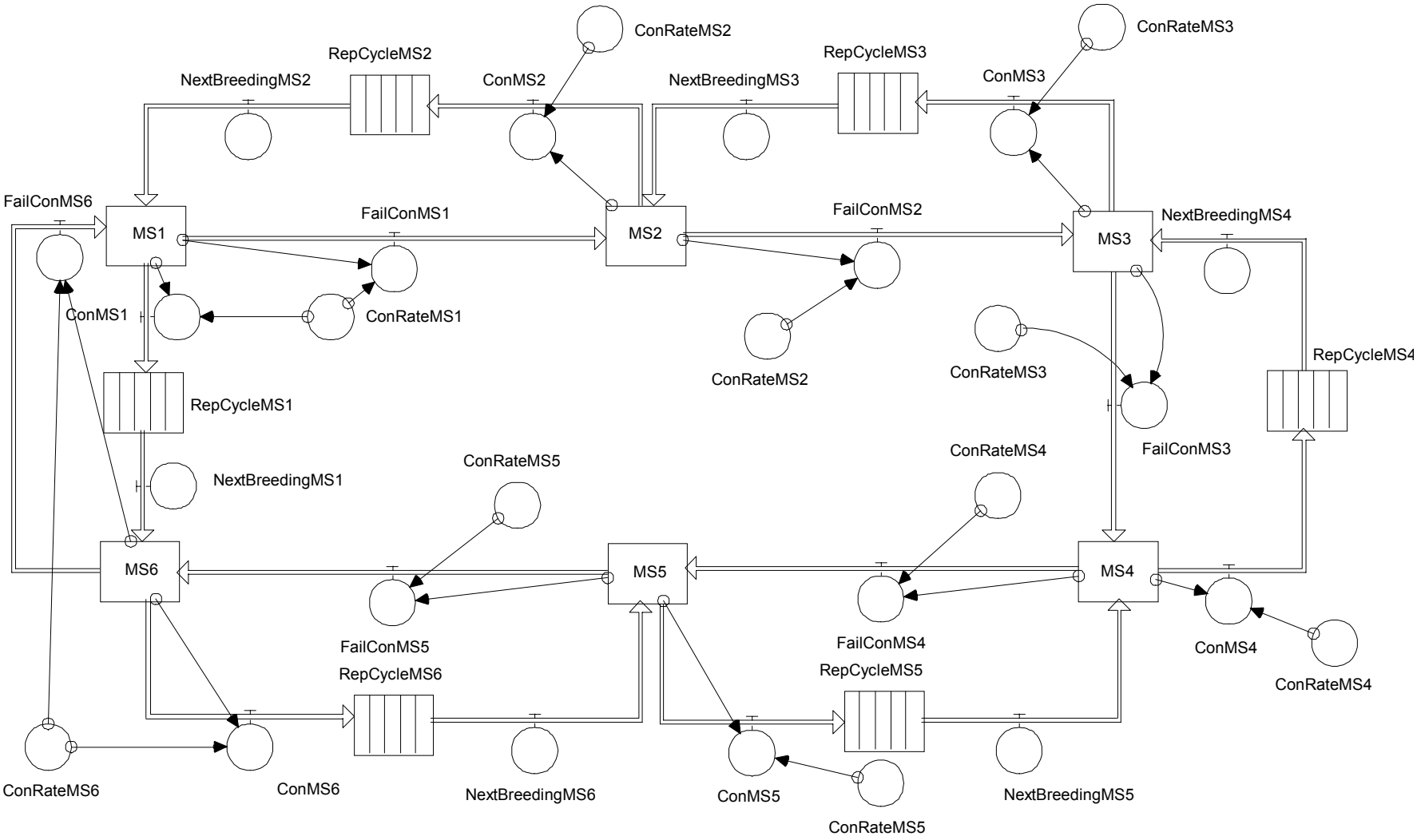

Figure A.1. Forrester-Diagramm of the simulation model used to assess the effect of an aseasonal breeding regime on the distribution of pregnancies in goat herds.

```
INFLOWS:
    NextBreedingMS5 = CONVEYOR OUTFLOW
    FailConMS3 = (1-ConRateMS3)*MS3
OUTFLOWS:
    FailConMS4 = (1-ConRateMS4)*MS4
    ConMS4 = ConRateMS4*MS4

MS5(t) = MS5(t - dt) + (NextBreedingMS6 + FailConMS4 - FailConMS5 - ConMS5) * dt“
INIT MS5 = 0
INFLOWS:
    NextBreedingMS6 = CONVEYOR OUTFLOW
    FailConMS4 = (1-ConRateMS4)*MS4
OUTFLOWS:
    FailConMS5 = (1-ConRateMS5)*MS5
    ConMS5 = ConRateMS5*MS5

MS6(t) = MS6(t - dt) + (NextBreedingMS1 + FailConMS5 - FailConMS6 - ConMS6) * dt“
INIT MS6 = 0
INFLOWS:
    NextBreedingMS1 = CONVEYOR OUTFLOW
    FailConMS5 = (1-ConRateMS5)*MS5
OUTFLOWS:
    FailConMS6 = (1-ConRateMS6)*MS6
    ConMS6 = ConRateMS6*MS6
RepCycleMS1(t) = RepCycleMS1(t - dt) + (ConMS1 - NextBreedingMS1) * dt“
INIT RepCycleMS1 = 0“
    TRANSIT TIME = 4“
    INFLOW LIMIT = INF“
    CAPACITY = INF
INFLOWS:
    ConMS1 = ConRateMS1*MS1
OUTFLOWS:
    NextBreedingMS1 = CONVEYOR OUTFLOW

RepCycleMS2(t) = RepCycleMS2(t - dt) + (ConMS2 - NextBreedingMS2) * dt“
INIT RepCycleMS2 = 0“
    TRANSIT TIME = 4“
    INFLOW LIMIT = INF“
    CAPACITY = INF
INFLOWS:
    ConMS2 = ConRateMS2*MS2
OUTFLOWS:
    NextBreedingMS2 = CONVEYOR OUTFLOW

RepCycleMS3(t) = RepCycleMS3(t - dt) + (ConMS3 - NextBreedingMS3) * dt“
INIT RepCycleMS3 = 0“
    TRANSIT TIME = 4“
    INFLOW LIMIT = INF“
    CAPACITY = INF
INFLOWS:
    ConMS3 = ConRateMS3*MS3
OUTFLOWS:
    NextBreedingMS3 = CONVEYOR OUTFLOW

RepCycleMS4(t) = RepCycleMS4(t - dt) + (ConMS4 - NextBreedingMS4) * dt“
INIT RepCycleMS4 = 0“
    TRANSIT TIME = 4“
    INFLOW LIMIT = INF“
    CAPACITY = INF
INFLOWS:
    ConMS4 = ConRateMS4*MS4
OUTFLOWS:
```

NextBreedingMS4 = CONVEYOR OUTFLOW

RepCycleMS5(t) = RepCycleMS5(t - dt) + (ConMS5 - NextBreedingMS5) * dt“
INIT RepCycleMS5 = 0“
TRANSIT TIME = 4“
INFLOW LIMIT = INF“
CAPACITY = INF
INFLOWS:
ConMS5 = ConRateMS5*MS5
OUTFLOWS:
NextBreedingMS5 = CONVEYOR OUTFLOW

RepCycleMS6(t) = RepCycleMS6(t - dt) + (ConMS6 - NextBreedingMS6) * dt“
INIT RepCycleMS6 = 0“
TRANSIT TIME = 4“
INFLOW LIMIT = INF“
CAPACITY = INF
INFLOWS:
ConMS6 = ConRateMS6*MS6
OUTFLOWS:
NextBreedingMS6 = CONVEYOR OUTFLOW

Parameters (conception rates)

ConRateMS1 = 0.962
ConRateMS2 = 0.827
ConRateMS3 = 0.857
ConRateMS4 = 0.889
ConRateMS5 = 0.930
ConRateMS6 = 0.861

Lebenslauf

Berufliche Tätigkeit

Seit 05/1999	**Systementwickler** im Verkaufsbereich der Otto-Versand GmbH, Hamburg.
10/1998 - 04/1999	**SAS-Anwendungsentwickler** in den Bereichen Data Warehouse, Database Marketing und Data Mining für die HMS GmbH, Heidelberg ● Entwicklung und Betreuung von Informationssystemen unter Verwendung objektorientierter Techniken ● Explorative und prädiktive statistische Datenanalysen ● Durchführung von Data Mining Projekten zur Entwicklung von Scoring-Systemen im Kreditwesen.
04/1997-11/1997	**Wissenschaftlicher Mitarbeiter** in einem BMBF-finanzierten Projekt zur Deichrückverlegung in der Elbtalaue bei Lenzen, Brandenburg. ● Datenbankorganisation; Integration von räumlichen Felddaten in ein GIS.
10/1991-03/1997	**Wissenschaftlicher Mitarbeiter** am Lehrstuhl für Nutztierökologie, Humboldt-Universität zu Berlin. ● Lehrtätigkeit im Bereich extensive Weidewirtschaftssysteme in den Tropen, Populationsökologie, Modellbildung in der Ökologie. ● Forschungsarbeit in den folgenden Bereichen: Mathematische Modellierung von bio-ökonomischen Prozessen unter Unsicherheit; Produktivitätsanalyse extensiver Weidewirtschaften; Ressourcen-degradation in den Trockengebieten Afrikas; Integration von Fernerkundungs- und GIS-Daten zur Modellierung von Entscheidungsproblemen in der Landnutzungsplanung.
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08/1990-11/1990	**Freiberufliche Tätigkeit** im Rahmen des "*Zentralen Weidelandprojektes, Somalia (GTZ)*", Institut für Tierproduktion der Technischen Universität Berlin
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05/1989-09/1991	**Studentischer Mitarbeiter** am Institut für Sozialökonomie der Agrar-entwicklung der Technischen Universität Berlin.

Promotion

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Studium

10/1987-07/1991	**Hauptstudium** der Agrarwissenschaften an der Technischen Universität Berlin; Studienschwerpunkt: Agrarökonomie; Thema der Diplomarbeit: "*Effizienz, Nachhaltigkeit und Modernisierung pastoraler Wirtschaftssysteme in Kenia*".
10/1986-09/1987	**Betriebspraktikum** in der Lehr- und Versuchsstation oberer Hardthof in Gießen und auf einem Milchviehbetrieb in Hamburg.

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Schulbildung

1976-1983	Lycée Franco-Allemand in Saarbrücken. Abschluß: Abitur
1971-1975	Belgische Grundschule in Kigali/Rwanda

Stipendien

07/1994-12/1994	Stipendium des Deutschen Akademischen Austauschdienstes (DAAD) zur Wahrnehmung eines Forschungsaufenthaltes an der Texas A&M University, USA. Spezialisierung auf mathematische Modellierungsmethoden und geographische Informationssysteme.

Eidesstattliche Erklärung

Hiermit erkläre ich eidesstattlich, daß die vorliegende Dissertation selbständig und ohne Hilfe Dritter verfaßt wurde, auch in Teilen keine Kopie anderer Arbeiten darstellt und die benutzten Hilfsmittel und Literatur vollständig aufgeführt sind.

Ingo Hary